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TAXONOMY AND SEASONAL DYNAMICS OF HELMINTHS IN *GAMMARUS LACUSTRIS* IN COOKING LAKE, ALBERTA

by

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A THESIS

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled Taxonomy and Seasonal Dynamics of Helminths in Gammarus lacustris in Cooking Lake, Alberta submitted by Michael Denny in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

ABSTRACT

The composition and seasonal dynamics of the helminth fauna of Gammarus lacustris population in Cooking Lake, Alberta were studied over a year and a half period from October 1965 to March 1967.

A total of twelve species of helminths, including eight cestodes, one nematode and three acanthocephalans, were recovered. Of these, eleven were new host records and nine assigned to an intermediate host species for the first time.

Adults of all twelve helminths were raised in experimentally infected birds and the life cycles of five were completed in the laboratory. The larvae are described as fully as possible, and the developmental period in the gammarids, prepatent period and life span of the adults are given for many of the helminths.

The stages of development of the two most extensively occurring helminths, Lateriporus skrjabini and Polymorphus marilis, were traced in more detail.

The gammarids are probably the main intermediate host for seven or eight of the helminths but not for the others of which three were found in other local aquatic invertebrates.

All but one of the more frequently occurring helminths survive the winter in the gammarids providing a nucleus of infection for wildfowl in the spring.

The seasonal dynamics and ecology of L. skrjabini and P. marilis were studied more extensively.

The seasonal distribution of L. skrjabini cysticercoids in the parent gammarids is bimodal, indicative of two generations. The cysticercoid-bearing gammarids probably have relatively short life spans. The helminth does not survive the winter in the gammarid population. The seasonal distribution of P. marilis cystacanths reaches a single peak at the end of the summer in the parental gammarids. The population undergoes two generations, the second infecting the young gammarids. Cystacanth-bearing gammarids probably have relatively long life spans. The helminth survives the winter in the gammarids as acanthors.

A brief discussion on concurrent infections and mortality in infected gammarids is given.

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INTRODUCTION

> The modern approach to parasitology envisages an ecological complex formed by the parasite, the vector, the host and various features of the host's environment. But this complex is far more than the sum of its parts.
>
> - Noble and Noble (1961, page 602).

One approach to ecological parasitology involves a long term investigation of the entire helminth fauna in a community. Wiśniewski (1958) and his co-workers (Jarecka, 1958, 1960, 1961; Rybicka, 1958; Styczyńska, 1958; Sulgostowska, 1958; et al. attempted this sort of study on some lakes in Poland, particularly Lake Drużno. The major aims of the study were to find the most typical and dominant parasite species of the community and to elucidate the paths of their circulation among the members of the community.

A similar long term study of the circulation of helminths in various aquatic habitats in the Edmonton area has been underway at the University of Alberta since 1961. The main sampling areas for this study have been Cooking and Hastings Lakes, located thirty five miles east of Edmonton, Alberta. These are two of a large number of shallow lakes or sloughs around Edmonton which serve as breeding or resting grounds for many migratory water birds, including some ten to fourteen species of ducks and geese, four species of grebes, six species of gulls and terns, five species of shorebirds and two species of rails.

Thus far, studies have been completed on the helminths of grebes (Gallimore, 1964), coots (Colbo, 1965), lesser scaup and ruddy ducks (Graham, 1966). In addition, the general limnology of the lakes

was investigated by Kerekes (1965). However, at the start of this study in 1965, no work had been done on the elucidation of the life cycles of any of the parasites nor had the helminths of any invertebrates been investigated. Gammarids were known to be a very important item of food for many water birds (Gallimore, 1964; Colbo, 1965; Graham, 1966). They were known to harbour many larval helminths (Table I), and their biology had been studied by Menon (1966). Therefore, Gammarus lacustris Sars (G. l. lacustris, according to Bousfield, 1958), the only gammarid in the local lakes, was chosen for study.

Previous studies at the University of Alberta have indicated the value of following the seasonal variation in abundance of the parasites in the host population, and correlating changes observed with changes in the environment. In this way, the effects of factors like the environmental temperature, changes in food habits, moulting, migration or hibernation of the host, etc., can be investigated.

Literature on the seasonal dynamics of the parasite fauna of invertebrates (other than trematode larvae in molluscs) is scarce. Only two reports have dealt with the parasites of amphipods. Hynes (1955), in conjunction with his studies on the life cycle of G. lacustris in Britain, recorded the seasonal incidence of infection with Polymorphus minutus. His information suggested that the acanthocephalan population interfered with moulting and breeding in the female, and could be a factor in inducing the violent fluctuations in numbers of G. lacustris that had been recorded by Reid (1951). Shteyn (1957), in his studies of the parasitology of benthic arthropods in some lakes in Karelia, reported high peaks of infection with trematode larvae in amphipods in July.

The dual purpose of the present study was therefore to ascertain the composition and seasonal dynamics of the helminth fauna of Gammarus lacustris.

TABLE I

HELMINTHS REPORTED FROM *GAMMARUS*

Parasite species	Host species	Authors
TREMATODA		
Crepidostomum metoecus	*G. pulex*	Awachie (1966)
Nicolla gallica	*G. pulex*	Timon-David (1965)
Orchipedum tracheicola	*G. lacustris*	Huebner (1965 - personal communication)
CESTODA		
Cyathocephalus truncatus	*G. pulex*	Awachie (1966)
Fimbriaria fasciolaris	*G. pulex*	Jarecka (1958)
Hymenolepis abortiva	*G. pulex*	Shteyn (1958)
Hymenolepis collaris	*G. pulex*	Joyeux (1926)
Hymenolepis gracilis	*G. pulex*	Dubinina (1953)
Hymenolepis microsoma	*G. locusta*	Belopolskaya (1952)
Hymenolepis tenuirostris	*G. pulex*	Linstow (1892)
Lateriporus teres	*G. pulex*	Linstow (1892), Spassky (1954), Uspenskaya (1960)
NEMATODA		
Cystidicola farionis	*G. pulex*	Awachie (1966)
Streptocara crassicauda	*G. lacustris*	Garkavi (1949a)
Tetrameres fissispina	*G. pulex*	Linstow (1909), Garkavi (1949b)
ACANTHOCEPHALA		
Echinorhyrnchus polymorphus	*G. locusta*	Luther (1904)
Echinorhyrnchus truttae	*G. pulex*	Luhe (1911), Awachie (1966)
Polymorphus magnus	*G. lacustris*	Petrochenko (1949)
Polymorphus minutus	*G. duebeni*	Hynes (1955)
	G. lacustris	Hynes (1955)
	G. pulex	Scheer (1934), Hynes and Nicholas (1957), Crompton (1964)

MATERIALS AND METHODS

Field Collections

Cooking Lake was selected as the study area because most of the birds of the previous studies had been taken there and ecologically, the lake closely resembled Big Island Lake, the lake in which Menon (1966) studied the ecology of Gammarus lacustris.

Cooking Lake is a highly productive eutrophic lake with a surface area of 35.12 Km^2, and a maximum depth of 3.5 metres (Kerekes, 1965). The frequent winds prevent thermal stratification in such a shallow lake. The entire shoreline is dominated by emergent vegetation, mainly cattail (Typha latifolia) and reed grass (Phragmites communis). The submergent vegetation, which becomes established after the emergent vegetation, is chiefly Potamogeton spp, Ceratophyllum demersum, Myriophyllum exalbescens and Lemna trisulca. Occasional floating clumps of Lemna minor are found.

Amphipods, G. lacustris and Hyalella azteca, and chironomid larvae are the dominant larger invertebrates. Leeches, oligochaetes and insects are also common. Planktonic crustacea (ostracods, cladocerans and copepods) are common in the summer months and at times very abundant during the "algael blooms."

During the winter months the lake is completely covered with ice, which reaches some three feet in thickness towards the end of the winter. In 1965-1966 the ice cover lasted from the last week of October to the last week of April. The seasonal variation in temperature of the lake water, taken six inches from surface, is shown in Fig. 1. Consider-

able depletion of plant and animal life occurred in the months of March and April, when there was no demonstrable oxygen in the lake and the hydrogen sulphide level was high.

Gammarids were collected during the winter months by breaking through the ice with a needle bar and spade, and scooping up the very top layers of the bottom mud with a dip net. The gammarids, which were at the surface of the mud, could then be washed clear of the mud. The few gammarids that were observed swimming freely around in the water were collected with the dip net.

In the summer months gammarids were easily collected with a dip net.

The thousand or so gammarids collected were brought back to the laboratory alive in buckets and set up temporarily in aerated aquaria with mud and a little vegetation, when possible, from the lake.

Some of these gammarids were autopsied qualitatively, particularly during the first summer of the study, to become acquainted with the host and its helminth fauna and to standardise a procedure to be used in a seasonal study of the gammarids and their parasites. The treatment adopted was as follows:

The gammarids to be autopsied were narcotised for two minutes in 50% alcohol, sexed by the presence of calceoli on the flagellum of the second antennae in males or oostegites in females, measured by the method described by Menon (1966) and the reproductive state of the females (pre-reproductive, ovigerous, or post-reproductive) recorded. The sex was recorded only for those gammarids 10 mm. or longer, since it was difficult to determine the sex of smaller individuals.

The type, number, and stage of maturity were recorded for all the helminths encountered. Many of the smaller early stages of development were probably overlooked. This was plainly evident, when, during March and April, 1967, acanthors and acanthellae were specifically looked for and found in much greater abundance than had been found earlier in the winter (page 88).

The cysticercoids of Lateriporus clerci, L. mathevossianae and L. skrjabini were morphologically distinguishable; however, their identities were confirmed by noting the number and size of rostellar hooks in temporary hook squashes. The hymenolepid cysticercoids were not readily distinguishable; therefore permanent hook preparations, in aqua-mount sealed with tar, were made for representative specimens from each infected gammarid.

The nematodes were fixed in glycerine-alcohol and mounted in glycerine-jelly.

It became clear that there were three reasonably distinct forms of the uneverted cystacanths. The form was noted in every cystacanth obtained and for a long while each one was everted in warm water and fixed in A. F. A. However, later, time did not permit the evertion and fixation of every one, so only occasional ones were kept, particularly those in which there was doubt as to their morphological type. The cystacanths preserved were dehydrated in alcohol, then cleared and examined in xylene. To carry out an accurate study of the proboscis armature (the number of rows of hooks, the number of hooks in each row and the size of the largest hook) the dehydrating and clearing had to be gradual.

In connection with the seasonal studies, to obtain a sample

representative of the gammarids throughout Cooking Lake, collections were made in three localities:

1) a small bay, supporting much submergent vegetation and encircled by beds of reeds and cattails. More ducks were observed to be associated with this bay than with any other locality of the lake. Gammarids were taken randomly from all parts of the bay from June to October, 1966.

2) a large bay, most of which had a mud bottom. Gammarids were collected from in and just above the mud from October, 1965 to May, 1966.

3) the main portion of the lake, in which collections were made along the junction of the emergent and submergent vegetation near the shore from October, 1965 to December, 1966.

Gammarids were sampled at two of these three localities twice each month when the lake was ice-covered, and four times each month when the lake was ice-free. Collections were begun in October, 1965 and ended in October, 1966. Further collections were made in December, 1966 and in April, 1967 for comparison with the preceding year.

These collections were set up in aquaria in the laboratory as previously described. Within the next 24 hours as many gammarids as possible were autopsied. For most of the year, this sample was drawn from the entire population, but from June to September inclusive the samples were drawn only from the parental generation. On some occasions a sample of some of the larger young were also autopsied.

On four occasions in July and August, the proportion of young in the population was determined in a random sample of about 400

gammarids.

In addition to the regular collections, on two occasions during the summer gammarids were collected from near the center of the lake as well as from the regular collecting localities near the shore to see whether there was any difference in the infection rates of the more abundant helminth species.

Laboratory Experiments

In order to identify the larval helminths found in the gammarids, and to elucidate the time taken for development of the adult to aid in the interpretation of the ecological data, a series of infection experiments were conducted. The birds used in these experiments were domestic ducks and chickens as well as wild ducks, coots and gulls. The wild birds were raised in the laboratory from eggs collected from nests in the vicinity of Cooking Lake.

The eggs taken from these nests were individually wrapped in down and/or cotton-wool, placed in buckets and transported as quickly as possible, often in a heated car, to the laboratory, where they were placed in a commercial incubator. The hatched young were kept in the incubator for 24 hours before being removed, wing-tabbed, taught to feed, and placed in cages warmed by brooder lamps. Warmth was very important, particularly for the first 2 weeks; an environmental temperature of 29.4-32.2 C being most suitable.

All the birds were fed on non-medicated turkey starter crumbles, except for the gulls which were given a variety of meats.

Some individuals of all the species of birds were fed large

numbers of gammarids offered to them in a petri dish. This procedure provided adults of all the gammarid-borne larval types. Single doses of specific larval types dissected from gammarids were fed to other birds with an eye dropper. These birds were killed and autopsied after different periods of time to obtain information on the length of the pre-patent period and life span of the adult helminths. In addition, in some instances, daily records were kept of the parasite material passed out with the faeces of infected birds. Not only did this augment the study on the time of development of the various stages, but also furnished an insight into the manner by which infective eggs are discharged and become available to the gammarids.

At autopsy, the number and state of maturity of any helminths present were recorded. The cestodes were regarded as mature if oncospheres were present in the uterus. The state of the ovary and the presence of immature or mature acanthors were noted for the acanthocephalans to provide an estimate of the degree of maturity.

All the helminths recovered were fixed in A. F. A. Some individuals of each species of cestode and acanthocephalan were stained. A variety of staining techniques were employed, especially for the taxonomically difficult hymenolepids. The few nematodes obtained were cleaned in glycerine-alcohol and mounted in glycerine-jelly.

To aid in the identification of the adult worms, specimens were compared directly with specimens found in birds naturally infected in the field. Most of these birds had been collected in the Cooking Lake region by other workers.

In an attempt to complete the life cycle of the gammarid-borne

helminths entirely in the laboratory as well as to elucidate the time of development of some of the helminths in the gammarids a series of infection experiments was conducted with gammarids.

Gammarids in which no infection could be detected in the body cavity, by close scrutiny of well illuminated individuals, were used in most of the infection experiments. Laboratory-raised young gammarids were also used. A few gammarids, observably infected with the conspicuous cysticercoid of Lateriporus or cystacanths of Polymorphus were also selected to test the possibility of superimposed infections.

The gammarids were exposed to the infective material (gravid segments of cestodes, gravid female acanthocephalans, or a suspension of eggs) in a small amount of lake water in a 4" fingerbowl. After exposure, the gammarids were rinsed, then maintained in 8" fingerbowls containing tapwater with a little mud and submergent vegetation from the lake, aerated by a breaker stone connected to an air-pump. The mud used was dried for several weeks in the laboratory to destroy all helminth eggs susceptible to desiccation.

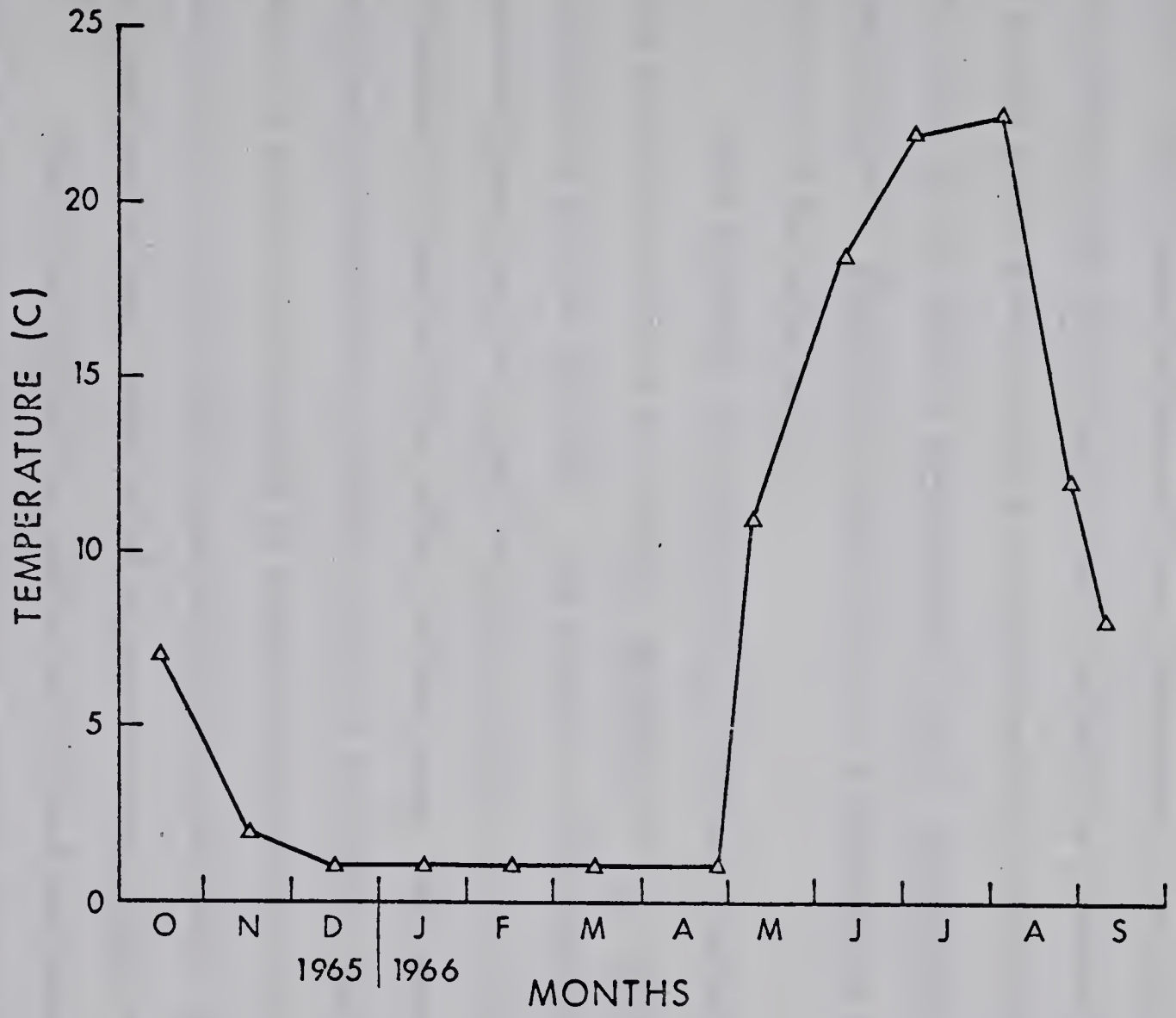
Gammarids were examined at intervals after exposure to infection and the number and developmental stage of any helminth larvae were recorded. Since there is no previous description of the stages of development of any of these helminths, the larvae found were compared to developmental stages of related parasites.

The 5 stages of development recognised by Voge and Heyneman (1957) in the development of Hymenolepis nana and Hymenolepis diminuta were used for the cysticercoids. These stages are: 1) a solid ball of

cells, 2) a hollow ball of cells, 3) an elongated body with little differentiation except for the scolex primordium, 4) the body differentiated and the scolex partly withdrawn, and 5) the fully developed cyst with scolex completely withdrawn.

The cystacanths were divided into developmental stages corresponding to those of Polymorphus minutus (Hynes and Nicholas, 1957; figure 1, page 386). These stages are: 1) a spherical, bright orange ball of cells with conspicuous giant nuclei surrounding a central nuclear mass (Hynes and Nicholas' drawing F, the fully developed acanthor), 2) an elongated body with the crenulated, ridged proboscis completely everted (the acanthella, figure K), and 3) the fully developed, lemon-shaped cyst with proboscis, fore-body and posterior end completely invaginated into the hind-body (the cystacanth, figure N).

Figure 1 Seasonal variation in temperature of Cooking Lake (temperatures taken 6" below surface)


TEMPERATURE (C)
25
20
15
10
5
0
O
N
D
J
F
M
A
M
J
J
A
S
1965
1966
MONTHS

TAXONOMY AND LIFE CYCLES

A total of twelve species of helminths, including eight cestodes, three acanthocephalans and one nematode, were recovered from gammarids from Cooking Lake. Data on the extensity and intensity of infection of the helminth species are presented in Table II. Although the cestode Fimbriaria fasciolaris was not found in the autopsies of gammarids, adults were recovered from laboratory birds fed on gammarids, and cysticercoids were raised experimentally in gammarids. Adults of all twelve species were raised in experimentally infected birds, and the life cycles of five species (Lateriporus clerci, Lateriporus skrjabini, Hymenolepis B, Fimbriaria fasciolaris and Polymorphus marilis) were completed in the laboratory.

The material from Gammarus, including developmental stages of the two most common species (L. skrjabini and P. marilis), are described as fully as possible. The adults, on the other hand, are described less completely with emphasis on the characteristics that distinguish the species from others of the group. All measurements are given in millimeters and were made on specimens fixed in A. F. A., cleared in xylene and mounted in Canada balsam unless otherwise stated. Measurements on the larger gammarid-borne parasites, the lateriporids and acanthocephalans, were taken on worms from single-worm infections.

Host records for the adults are divided into three categories: local records, including those of Gallimore (1964), Colbo (1965), Graham (1966) and others in the files of the Department of Zoology, University of Alberta, from birds or mammals collected around Edmonton,

Alberta; experimental records, those raised in the laboratory in this study; and records from elsewhere, based on the lists in McDonald, 1965.

Scientific names of waterfowl are as listed by Delacour and Mayr (1945), the names of other North American birds are taken from the A.O.U. checklist (1957), and the names of other birds are taken from Peterson et al.(1954).

TABLE II

HELMINTHS FOUND IN 7135 GAMMARIDS FROM COOKING LAKE, ALBERTA FROM OCTOBER 1965 - SEPTEMBER 1966

Parasite	Extensity (percent)	Intensity mean (range)	Relative* abundance
Lateriporus clerci	0.2	1.0 (1-4)	0.2
Lateriporus mathevossianae	0.7	1.0 (1-3)	0.7
Lateriporus skrjabini	3.7	3.4 (1-21)	12.6
Hymenolepis spiralibursata	0.01	11.0 (11.0)	0.11
Hymenolepis tuvensis	0.04	13.3 (7-20)	0.53
Hymenolepis A	0.2	20.5 (13-30)	4.1
Hymenolepis B	0.5	25.0 (8-70)	12.5
Fimbriaria fasciolaris	-	-	-
Streptocara crassicauda	0.1	1.0 (1.0)	0.1
Polymorphus contortus	0.8	1.0 (1-4)	0.8
Polymorphus marilis	12.7	1.1 (1-9)	12.8
Polymorphus paradoxus	0.8	1.0 (1-3)	0.8

*extensity times mean intensity

CESTODA

The cysticercoids found in the haemocoel of the gammarids could be separated into two distinct groups. The first group, consisting of large, white crinkle-walled cysticercoids, developed into adults of three species of Lateriporus (L. clerci, L. mathevossianae and L. skrjabini) when fed to various species of birds in the laboratory. The cysticercoids of the three species could be distinguished by their size and shape, the degree of convolution of the strobila within the cyst and by the number, size and shape of rostellar hooks.

The adults of the three species could be distinguished by the length of the mature strobila, the length, structure and armature of the cirrus, the structure of the uterus and the number, size and shape of the rostellar hooks.

Lateriporus clerci (Johnston, 1912)

Description of the cysticercoid

Inverted cysticercoid white, crinkle-walled, 1.515 - 2.294 (1.925) long by 0.666 - 0.960 (0.777) wide, containing a much convoluted strobila (measurements made on 12 unfixed specimens placed in water for no longer than three minutes).

Total length of everted cysticercoid 4.2 - 4.8 (4.5). Scolex prominent, 0.300 - 0.360 (0.335) long by 0.310 - 0.385 (0.355) wide, with four suckers 0.210 - 0.240 (0.228) x 0.180 - 0.210 (0.197). Rostellar sac 0.270 - 0.300 (0.283 long). Rostellum, measured from its base within the rostellar sac, 0.450 - 0.480 (0.462) long, armed with 16 - 19 hooks (usually 16, rarely 12) 0.208 - 0.230 (0.218) long; blade 0.105 - 0.115 (1.109) long and handle 0.107 - 0.119 (0.111) long. Neck 0.240 - 0.263 (0.255) wide at its narrowest region. Strobila 3.427 - 3.670 (3.574) long by 0.290 - 0.305 (0.297) wide, segmented internally and externally, with remnants of cyst attached to its posterior end. (Hook measurements based on 35 specimens, other measurements based on 12 specimens.)

Development in gammarids

Gammarids were infected with gravid proglottids from worms grown in laboratory birds, completing the life cycle of the parasite entirely in the laboratory. Gammarids were observed to harbour some fully developed cysticercoids when first examined 35 days after being exposed to gravid proglottids.

Host records for cysticercoid

Gammarus lacustris (this study)

Description of the adult

Mature worms 80 - 100 long and 2.2 - 2.4 in maximum width (gravid proglottids). Scolex 0.520 - 0.550 long by 0.460 - 0.510 wide, with suckers 0.200 - 0.350 x 0.250 - 0.400. Rostellar sac 0.530 - 0.580 long; rostellum, measured from its base within the rostellar sac, 0.550 - 0.610 long bearing 16 hooks, 0.210 - 0.226 long with blade 0.105 - 0.112 long. Neck 0.285 - 0.315 wide. Proglottids that contain the testes immediately before they break up 0.770 - 0.820 wide by 0.390 - 0.420 long. Cirrus sac 0.375 - 0.440 long by 0.110 - 0.130 in maximum width, opening into genital atrium situated mid way along the edge of the proglottid, with medial end directed obliquely forwards to anterior part of proglottid and reaching a little under half way across the proglottid. Genital atria often everted. Cirrus, when fully extended, 0.300 - 0.450 long, has a distinctly bulbous base covered with large spines 0.01 long and a thin distal segment covered with smaller spines. Testes 15 - 17 in number, 0.060 - 0.070 in maximum diameter, situated in mid posterior region of proglottid. Vas deferens coiled in mid anterior region of proglottid. Ovary central. Vagina slightly convoluted, opens into genital atrium immediately ventral to cirrus sac. Shell gland 0.07 - 0.08 mm in maximum diameter. Uterus, early in development, plate-like, extending right across the mid portion of the proglottid, later enlarging to occupy most of the proglottid as one big bag. (Measurements based on seven specimens from Larus delawarensis.)

Development in gulls

A single mature specimen was found after an infection of 11 days in the only ring-billed gull (Larus delawarensis) exposed. Eggs from the gravid proglottids were infective to gammarids.

Host records for adult

Locally: Larus delawarensis, Larus pipixcan, Podiceps grisegena (mature adults); Fulica americana (immatures only).

Experimentally: Larus delawarensis (mature adults); did not become established in Aythya affinis, Melanitta deglandi.

Elsewhere: Aythya marila, Fulica atra, Larus canus, Larus ridibundus.

Lateriporus mathevossianae Ryzhikov and Gubanov, 1962

Description of the cysticercoid

Inverted cysticercoid white, crinkle-walled 1.976 - 3.071 (2.579) long by 1.200 - 1.850 (1.545) wide containing a slightly convoluted strobila (measurements made on 12 unfixed specimens placed in water for no longer than three minutes).

Total length of everted cysticercoid 3.9 - 4.2 (4.05). Scolex not very prominent, 0.455 - 0.480 (0.467) long by 0.665 - 0.689 (0.673) wide with four slightly cup-shaped suckers 0.225 - 0.260 (0.248) x 0.180 - 0.210 (0.196). Rostellar sac 0.390 - 0.460 (0.435) long. Rostellum contracted, armed with ten hooks 0.235 - 0.256 (0.248) long, blade 0.090 - 0.108 (0.098) long and handle 1.34 - 1.50 (1.46) long. Neck 0.500 - 0.518 (0.510) wide at its narrowest region. Strobila 1.725 - 2.100 (1.905) long by 0.525 - 0.542 (0.536) wide, segmented externally, with rudiments of segmentation internally, and with remnants of cyst attached to its posterior end. (Hook measurements based on 25 specimens, other measurements based on 12 specimens.)

Development in gammarids

Gammarids were infected with gravid proglottids from worms taken from wild birds. In the haemocoel, the oncosphere develops through stages resembling those of L. skrjabini reaching the fully developed cysticercoid in a minimum of 35 days at 23 C. (Table III indicates the approximate time taken to reach the various stages of development.)

Since the intensity of infection in naturally infected gammarids (a mean of 1.6, and a maximum of 4) is less than that recorded for the experimentally infected gammarids (a mean of 8.0, and a maximum of 23), the rate of development of the parasite in the naturally infected gammarids of Cooking Lake may be greater, at comparable temperatures, than that recorded in the experimentally infected gammarids.

Host records for cysticercoid

Gammarus lacustris (this study)

Description of the adult

Mature worms 10 - 15 long and 0.98 - 1.105 in maximum width (gravid proglottids). Scolex 0.850 - 0.950 long by 0.810 - 0.870 wide with suckers 0.250 - 0.290 x 0.300 - 0.345. Rostellar sac 0.700 - 0.760. Rostellum, measured from its base within the rostellar sac, 0.600 - 0.675 long, bearing 10 hooks 0.230 - 0.256 long, with blade 0.094 - 1.05 and handle 0.134 - 0.150 long. Neck 0.600 - 0.720 wide. Proglottids that contain the testes immediately before they break up, 0.930 - 0.950 wide by 0.230 - 0.250 long. Cirrus sac 0.350 - 0.370 long by 0.095 - 0.105 in maximum width, opening into genital atrium situated mid way along edge of proglottid with medial end directed forwards to the anterior part of the proglottid and reaching just underhalf way across the proglottid. Genital atrium never everted. Cirrus, when fully extended, 0.400 - 0.450 long, of about uniform diameter, covered with small spines. Testes 14 in number, 0.070 - 0.076 in diameter, concentrated largely at the lateral edges of the proglottid on either side of the ovary and shell gland. Vas deferens coiled in aporal anterior region of proglottid. Ovary lobular and central. Vagina narrow, slightly convoluted, opening into genital atrium

ventral to cirrus sac. Shell gland central, 0.08 - 0.09 in diameter, (Measurements based on 10 specimens from Melanitta deglandi.)

Development in ducks

Of the eight white-winged scoters (Melanitta deglandi) that were fed cysticercoids, only one became infected, from which three immatures were recovered after five days. These worms were ten mm in length and had well developed testes and ovary but no signs of eggs in the uterus. As no gravid worms were obtained it was not possible to complete the life cycle of the parasite in the laboratory.

Host records for adult

Locally: Melanitta deglandi (mature adults); Aythya affinis, Fulica americana (immatures only).

Experimentally: Aythya affinis, Melanitta deglandi (immatures); did not become established in Anas platyrhynchos, Aythya americana, Fulica americana.

Elsewhere: Melanitta fusca.

Lateriporus skrjabini Matevosian, 1946

Description of the cysticercoids

Inverted cysticercoid white, crinkle-walled, 1.117 - 2.220 (1.740) long by 0.700 - 0.925 (0.780) wide containing a slightly coiled strobila. (Measurements made on 12 unfixed specimens placed in water for not more than three minutes).

Total length of everted cysticercoid 2.480 - 2.60 (2.545). Scolex prominent, 0.360 - 0.405 (0.378) long by 0.480 - 0.510 (0.497) wide, with four suckers, 0.240 - 0.270 (0.258) x 0.090 - 0.125 (0.115). Rostellar sac 0.265 - 0.300 (0.284) long. Rostellum armed with 12-15

(usually 14) hooks; 0.161 - 0.186 (0.175) long, blade 0.075 - 0.083 (0.079) long and handle 0.093 - 0.105 (0.098) long. Neck 0.230 - 0.250 (0.242) wide at its narrowest region. Strobila 0.805 - 0.818 (0.810) long by 0.300 - 0.325 (0.314) wide, unsegmented internally, rudiments of segmentation externally and with remnants of cyst attached to its posterior end. (Hook measurements based on 65 specimens, other measurements based on 12 specimens.)

Development in gammarids

Gammarids were infected by eggs from worms grown in laboratory birds (so completing the life cycle of the parasite entirely in the laboratory) and from birds shot in the field. In tapwater the proglottids became distended, eventually burst and released large spherical eggs. Gammarids became infected when exposed to a suspension of eggs in water. Gammarids also avidly "attacked" the gravid proglottids and were often seen carrying a portion of the ripe strobila around in the aquaria. The oncosphere ingested by gammarids presumably penetrates through the gut wall and enters the haemocoel, where the cysticercoid develops.

The earliest stage observed in this study, at seven days, was a pear-shaped structure, 0.345 mm long, with a cavity and the embryonic hooks at the more rounded end. From day 12 - 16 the larva had reached its maximum length of 1.020 mm at which stage it was divided into three regions: large hollow rounded hind-body, long narrow tubular mid-body, and knob-like fore-body of dense cells which showed stages of differentiation of the structures of the scolex and hooks. On day 16 the scolex had begun to withdraw into the hind-body and on day 36 the fully developed cysticercoid had been formed. (Table III indicates the approximate time taken to reach the various stages of development.)

Whether these developmental times are similar to those of the parasite in the less heavily infected gammarids of Cooking Lake is questionable. The mean intensity of infection of naturally infected gammarids with both developmental stages and fully developed cysticercoids is 3.5. In the experimentally infected gammarids, on the other hand, the mean intensity of infection was 40. Clearly, then, the intensity of infection of laboratory gammarids was considerably greater than that of the naturally infected gammarids.

Voge and Heyneman (1957) reported that crowding in the intermediate host decreased the rate of development of Hymenolepis nana, although not of H. diminuta. The data from laboratory infections in the present study indicate that the rate of development of cysticercoids is greater in gammarids with a lower intenstiy of infection (Fig. 2) and is also greater in the larger gammarids (Fig. 3). Thus, it is possible that the rate of development of L. skrjabini in the naturally infected gammarids of Cooking Lake is greater, at comparable temperatures, than that recorded in laboratory infected gammarids.

The size of the cysticercoid varies according to the number in the gammarid from 1.17 - 2.22 x 0.7 - 0.93 in single infections to 0.95 - 1.3 x 0.56 - 0.7 in a multiple infection of 21.

Host records for cysticercoids

Gammarus lacustris (this study)

Description of the adult

Mature worm 100 - 120 long and 1.390 - 1.470 in maximum width (gravid proglottids). Scolex 0.650 - 0.700 long by 0.700 - 0.800 wide with four suckers 0.225 - 0.300 x 0.350 - 0.570. Rostellar sac 0.450 - 0.600 long. Rostellum, measured from its base within the rostellar sac, 0.495 - 0.545 bearing 14 hooks, 0.182 - 0.188 long with blade 0.081 - 0.083 and handle 0.101 - 0.105. Neck 0.330 - 0.345 wide. Proglottids that contain the testes immediately before they break up, 0.800 - 0.900 wide by 0.273 - 0.325 long. Cirrus sac 0.315 - 0.345 long by 0.110 - 0.130 wide (maximum size), opening into genital atrium situated midway along edge of proglottid, with medial end bending towards the anterior portion of the proglottid and reaching about midway across the proglottid. Genital atrium often everted. Cirrus when fully extended, 1.2 - 1.4 long, with a thickened base covered with spines and a very slender distal segment naked for the most part except for a bristled region at the tip. Testes 12 - 13 per proglottid, 0.065 - 0.088 in maximum diameter, situated in mid posterior region of the proglottid. Vas deferens coiled in anterior aporal region of proglottid. Ovary central; vagina, dilated medially into seminal receptaculum, opens into genital atrium ventral to the cirrus sac. Shell gland central, 0.70 - 0.76 in maximum diameter. Uterus early in development plate-like, extending right across the mid portion of the proglottid, later becoming constricted in centre, forming two sacs which come to occupy most of the proglottid. Outer envelope of egg, fresh in water, 0.142 - 0.150, inner envelope 0.070 - 0.079 and oncospheral membrane 0.020 - 0.024 (terminology after Rybicka, 1965). (Measurements based on 10 specimens from Aythya affinis.)

Development in ducks

Adults were raised in 18 scaup (Aythya affinis) and redheads (Aythya americana). Two scaup examined after four days were found to have several immature adults in which the testes were very prominent and there were no signs of a uterus containing eggs. A redhead examined after six days contained several immature worms with their testes partially broken up and the uterus containing some small immature eggs. On day eight, two scaup, and on day nine a redhead, contained some worms

that had their uteri filled with eggs, some of which showed embryonic hooks therefore were presumably mature. The terminal proglottids were still intact in many, but not all, of the worms. Two scaup and a redhead began to pass gravid proglottids in the faeces on day eight and nine respectively; clearly, gravid proglottids appear to be shed very soon after the first mature-looking eggs are observed. The proglottids shed from both hosts contained eggs that infected gammarids in the laboratory. The remaining birds autopsied (last one on day 14) all contained gravid worms.

Gravid proglottids were discharged in the faeces of two scaup and a redhead for 24 and 25 days respectively. Autopsy of the birds, after gravid proglottids had ceased to be passed in the faeces, revealed no worms. Thus the parasite has a prepatent period of eight to nine days and a life span of the adult of 32 - 34 days.

Host records for adult

Locally:	Aythya affinis, Aythya americana, Aythya valisineria (mature adults); Anas acuta, Anas discors, Anas strepera, Bucephala albeola, Bucephala clangula, Mareca americana, Melanitta deglandi, Podiceps caspicus, Podiceps grisegena, Oxyura jamaicensis (immatures only).
Experimentally:	Aythya affinis, Aythya americana (mature adults); Anas platyrhynchos, Anas platyrhynchos domesticus (Pekin strain)

(immatures only); did not become established in Anas discors, Anas platyrhynchos, Anas strepera, Anas platyrhynchos domesticus (Rouin strain), Melanitta deglandi.

Elsewhere: Aythya fuligula, Aythya marila, Anas crecca, Bucephala clangula.

The second group of cysticercoids found in gammarids were small, oval and smooth-walled; 15 - 50 of them were found embedded in a jelly-like mass in a single gammarid. When fed to laboratory birds they developed into five different adults: Fimbriaria fasciolaris, distinguished by its large size, minute scolex and fimbriated pseudoscolex, and four species of Hymenolepis, all belonging to the genus Microsomacanthus (recognised by Russian workers and Yamaguti (1958) but not by the majority of N. American and W. European authors), which could be separated from one another on the basis of their hooks, the structure of the cirrus and cirrus sac, eggs and method of apolysis (Table IV).

Their cysticercoids could be distinguished only by the size and shape of their rostellar hooks. Caution must be exercised here since H. abortiva, a helminth known to develop in gammarids (Jarecka, 1960) and reported from this region (Graham, 1966), and H. tuvensis, also reported from this region (Graham, 1966), are indistinguishable on the basis of hooks.

Hymenolepis spiralibursata Czaplinski, 1956

Descriptions of the cysticercoid

Inverted cysticercoid oval, smooth, 0.201 - 0.220 (0.210) long by 0.153 - 0.176 (0.165) wide. Rostellum armed with 10 hooks 0.028 - 0.030 (0.029) long, blade 0.003 - 0.005 (0.004) long, handle 0.024 - 0.026 (0.025) long. (Hook measurements made on five specimens, other measurements based on two unfixed specimens placed in water.)

Development in gammarids

No gammarids were exposed to eggs of the helminth in the laboratory.

Host records for cysticercoid

Macrocyclops albidus, *Acanthocyclops viridis*, *Mesocyclops leukarti*, *Anodonta piscinalis*, *Radix ampla*, *Radix auriculata*, *Radix ovata* and *Lymnaea stagnalis* (Jarecka, 1961). The last five (molluscs) are believed to act as transport hosts.

Gammarus lacustris (this study)

Description of the adult

Mature worms very small, 1.5 - 1.9 long with no more than 15 segments. Rostellum armed with ten hooks 0.028 - 0.030 long, blade 0.003 - 0.005 long, handle 0.024 - 0.026 long. Uterus saccular, contains more than 50 eggs, 0.033 - 0.037 in diameter. Gravid proglottids shed one at a time. (Description based on five specimens, two from domestic Pekin ducks and three from scaup).

Development in ducks

Two domestic Pekin ducks contained mature worms when examined six and 14 days after infection.

Host records for adult

Locally: Aythya affinis (mature adults).

Experimentally: Anas platyrhynchos domesticus (Pekin strain) (mature adults).

Elsewhere: Anas querquedula, Anas platyrhynchos, Anas platyrhynchos domesticus, Aythya ferina, Aythya nyroca,

Hymenolepis tuvensis (Spasskaya and Spassky, 1961)

Description of the cysticercoid

Inverted cysticercoid oval, smooth, 0.153 - 0.195 (0.170) long by 0.120 - 0.135 (0.125) wide, enveloped in layers of jelly-like material in which are embedded the embryonic hooks. Scolex 0.080 - 0.095 (0.087) wide with four prominent suckers, 0.035 - 0.043 (0.039) x 0.020 - 0.034 (0.029). Rostellum armed with ten hooks, 0.034 - 0.037 (0.036) long; blade 0.012 - 0.014 (0.013) long; handle 0.022 - 0.024 (0.023) long. (Hook measurements made on ten specimens, other measurements made on five unfixed specimens placed in water.)

Development in gammarids

Gammarids exposed to gravid proglottids, some of which were detached from the strobila, failed to become infected.

Host records for cysticercoid

Gammarus lacustris, Hyalella azteca (this study)

Description of the adult (Fig. 4)

Mature worm 18 - 25 long. Rostellum with ten hooks, 0.034 - 0.037 long, blade 0.012 - 0.014, handle 0.022 - 0.024 long. Cirrus 0.117 - 0.125 long, base within genital atrium covered with minute spines, "neck" covered with much larger spines, leading distally to

swollen region covered with small spines sharply tapering into a small naked end bulb. Uterus saccular, contains 20 - 25 eggs, 0.050 - 0.058 in diameter. Gravid proglottids shed one or two at a time. (Description based on ten specimens from scaup).

The adults raised in laboratory infections are identical to H. tuvensis collected from scaup in this region (Graham, 1966). They also agree well with the description of H. tuvensis by Spasskaya and Spassky (1960), but have slightly smaller hooks, lack the prominent guard mentioned in the original description, and have a smaller internal seminal vesicle.

Development in ducks

One scaup infected in the laboratory contained mature worms seven days later.

Host records for adult

Locally: Aythya affinis (mature adults).

Experimentally: Aythya affinis (mature adults), Anas platyrhynchos domesticus (Pekin strain), Gallus gallus domesticus (leghorn strain) (immature only).

Elsewhere: Anas falcata, Aythya fuligula, Bucephala clangula.

Hymenolepis A

Description of the cysticercoid

Inverted cysticercoid oval, smooth, 0.210 - 0.315 (0.260) long by 0.120 - 0.240 (0.155) wide, often enveloped by layers of jelly-like material in which are found embryonic hooks. Scolex 0.098 - 0.115 (0.108) wide with four prominent suckers 0.041 - 0.048 (0.046)

x 0.028 - 0.041 (0.036). Rostellum armed with ten hooks 0.039 - 0.043 (0.041) long, blade 0.012 - 0.015 (0.014), handle 0.025 - 0.029 (0.027) long. (Hook measurements made on 30 specimens, other measurements made on ten unfixed specimens placed in water.)

Development in gammarids

Gammarids exposed to gravid proglottids, some of which had been shed from the strobila, failed to become infected.

Host record for cysticercoid

Gammarus lacustris (this study)

Description of the adult (Fig. 5)

Mature worm 2.5 - 4.5 long and 0.475 - 0.515 in maximum width (gravid proglottids). Scolex 0.153 - 0.170 long by 0.197 - 0.250 wide with four suckers 0.092 - 0.109 x 0.054 - 0.065. Rostellar sac 0.179 - 0.190 long. Rostellum, measured from its base within the rostellar sac, 0.219 - 0.230 long, with expansion armed with ten hooks 0.039 - 0.043 long, with blade 0.012 - 0.015 and handle 0.025 - 0.029 long. Neck 0.109 - 0.117 wide. Proglottids that contain the testes immediately before they break up 0.143 - 0.147 wide by 0.085 - 0.100 long. Cirrus sac 0.219 - 0.230 in maximum length, opening into genital atrium situated on the anterior edge of proglottid with medial end extending nearly two thirds across the proglottid. Cirrus 0.101 - 0.109 long, tubular, densely covered with small spines except along one side (the inner side of the commonly curved cirrus), which remains naked. Testes three, arranged in a transverse row, 0.036 - 0.054 long by 0.025 - 0.032 wide (maximum size). Ovary central, two-lobed. Shell gland 0.041 - 0.055, in central posterior region of proglottid. Internal seminal vesicle occupying a little over half of the space in the cirrus sac. External seminal vesicle 0.050 - 0.069. Vagina with seminal receptaculum attached medially. Gravid uterus saccular, contains more than 50 eggs, 0.033 - 0.038 in diameter, invested one behind the other in a tube. Gravid proglottids shed one, two, or three at a time. (Measurements based on 20 specimens, 14 from scaup and six from redheads.)

Hymenolepis A is identical to the worms found by Gallimore (1965) from grebes and described as Nadejdolepis sp.

These characteristics do not fit any of the descriptions of species of Hymenolepis (especially those placed in Microsomacanthus) available to me. It most closely resembles H. jaegerskioeldi Fuhrmann, 1913. Since H. jaegerskioeldi is present in scaup in this region (Graham, 1966) a direct comparison was possible. The hooks of H. jaegerskioeldi (0.042 - 0.045) are larger, though the shape is very similar. The cirrus of H. jaegerskioeldi is shorter and covered all over with small spines, not having a naked side. The uterus in H. jaegerskioeldi is distinctly "U"-shaped and not saccular as in the specimens of this study.

Development in ducks

Mature worms were found in five scaup examined six to twelve days after infection. Immature worms were found in a redhead four days after infection but mature worms were found in another redhead examined ten days after infection.

Host records for adult

Locally:	Podiceps grisegena, Aechmophorus occidentalis (mature adults).
Experimentally:	Aythya affinis, Aythya americana (mature adults); Anas platyrhynchos domesticus (Pekin strain) (immatures only); did not become established in Fulica americana.

Hymenolepis B

Description of the cysticercoid

Inverted cysticercoid oval, smooth, 0.255 - 0.345 (0.310) long by 0.180 - 0.240 (0.220) wide, often enveloped by layers of a jelly-like material in which are found the embryonic hooks. Scolex 0.140 - 0.157 (0.149) wide with four prominent suckers 0.045 - 0.056 (0.052) x 0.036 - 0.047 (0.041). Rostellum armed with ten hooks 0.049 - 0.052 (0.051) long; blade 0.008 - 0.012 (0.010), handle 0.035 - 0.041 (0.038) long. (Hook measurements made on 45 specimens, other measurements made on ten unfixed specimens in water).

Development in gammarids

Gammarids examined seven days after infection were found to have immature cysticercoids (scolex formed but not yet invaginated into mid-body). Of the three gammarids examined on day eight, the only infected one had "mature" cysticercoids, infective to birds in the laboratory. All infected gammarids from day 11 to 220 (when the last one was autopsied) contained mature cysticercoids.

Host records for cysticercoid

Gammarus lacustris (this study)

Description of the adult (Fig. 6)

Mature worm 4.5 - 6.5 long and 0.375 - 0.390 in maximum width (gravid proglottids). Scolex 0.142 - 0.150 long by 0.179 - 0.194 wide, with suckers 0.087 - 0.095 x 0.036 - 0.047. Rostellar sac 0.179 - 0.190 long. Rostellum, measured from its base within the rostellar sac, 0.183 - 0.190 long, expanded distally and armed with ten hooks, 0.049 - 0.052 long with blade 0.008 - 0.012 long and handle 0.035 - 0.041 long. Neck 0.128 - 0.135 wide. Proglottids that contain the testes immediately before they break up 0.256 - 0.267 wide by 0.034 - 0.038 long. Cirrus sac 0.161 - 0.168 long (maximum size), opening into genital atrium situated on the anterior edge of the proglottid, medial end extending two thirds across proglottid. Cirrus 0.053 - 0.061 long, covered all over with spines, with "lips" present at the

wider distal end. Testes three, arranged in a transverse row 0.016 - 0.023 in maximum diameter. Ovary central. Shell gland aporal, 0.021 - 0.034 in diameter. Vagina with swollen medial region to which is attached the seminal receptaculum. Gravid uterus saccular, contains 13 - 19 eggs, 0.033 - 0.039 in diameter. Gravid proglottids shed in blocks of 9 - 14. (Measurements based on 12 specimens from scaup and eight from redheads.)

There appears to be no available description of a species of Hymenolepis which these specimens resemble at all closely. The size and general shape of the hooks resemble those of H. microsoma (Fuhrmann, 1913) but the size of the worm and the structure of the proglottids are very different.

Development in ducks

Mature worms were found in eight scaup examined 8 - 15 days after infection; 16 - 17 days after infection no worms were found. Immature worms with uteri filled with eggs in which no embryonic hooks were visible were found in a redhead examined five days after infection but mature worms were found in three others 6 - 12 days after infection (worms on the day six were shown to be infective to gammarids in the laboratory); 15 and 16 days after infection no worms were found. The prepatent period of the helminth in these two hosts, then is about six days and the life span of the adult about 15 days.

Host records for adult

Locally:	Melanitta deglandi (mature adults); Fulica americana (immatures only).
Experimentally:	Aythya affinis, Aythya americana (mature adults); Anas platyrhynchos domesticus

(Pekin strain) (immatures only); did not become established in Fulica americana.

Fimbriaria fasciolaris (Pallas, 1781)

Description of the cysticercoid

Inverted cysticercoid small, oval, smooth, 0.150 - 0.169 (0.158) long by 0.138 - 0.145 (0.142) wide, with a long gelatinous tail in which are found the embryonic hooks. Rostellum armed with ten hooks 0.021 - 0.022 (0.022) long, blade 0.007 - 0.009 (0.008), handle 0.013 - 0.015 (0.014) long. (Measurements made on six unfixed specimens placed in water.)

Development in gammarids

Gravid proglottids from worms grown in the laboratory birds were infective to gammarids, completing the life cycle entirely in the laboratory. Mature cysticercoids were found in the gammarids when first examined 13 days after infection. Gammarids autopsied 84 days after infection also contained cysticercoids. In spite of the abundance of infective material used, both the extensity (20%) and the mean intensity of infection (5) were low.

Gravid proglottids were also infective to Hyalella azteca. Immature cysticercoids were obtained from hyalellids examined five days after infection; however, those examined after eight days contained mature cysticercoids which were infective to laboratory birds. The extensity (over 50%) and the mean intensity of infection (65) suggest that hyalellids are a more suitable host than gammarids. Infected hyalellids have been kept alive in the laboratory for 11 months.

Host records for cysticercoid

Acanthocyclops viridis, Diaptomus vulgaris, Eucyclops serrulatus, Macrocyclops albidus, Gammarus lacustris and experimentally in Cyclocypris laevis and Cypridopsis vidua (Garkavi, 1950; Jarecka, 1958).

Hyalella azteca (this study)

Description of the adult

Since the parasite is well known, adequately described and easily distinguished from other local helminths, it will not be described here.

Mature adults were found in a scaup when first examined ten days after infection. Gravid proglottids from these worms were infective to gammarids in the laboratory. Gravid proglottids were first voided in the faeces of two scaup 11 days after infection.

Host records for adult

Locally:	in a wide variety of local ducks.
Experimentally:	Anas platyrhynchos domesticus (Pekin strain) (mature adults).
Elsewhere:	Species from eight orders: Anseriformes, Charadriiformes, Falconiformes, Galliformes, Gruiformes, Pelecaniformes, Piciformes, and Podicipediformes.

TABLE III

DEVELOPMENT OF LATERIPORUS SKRJABINI IN GAMMARIDS AT 23 C

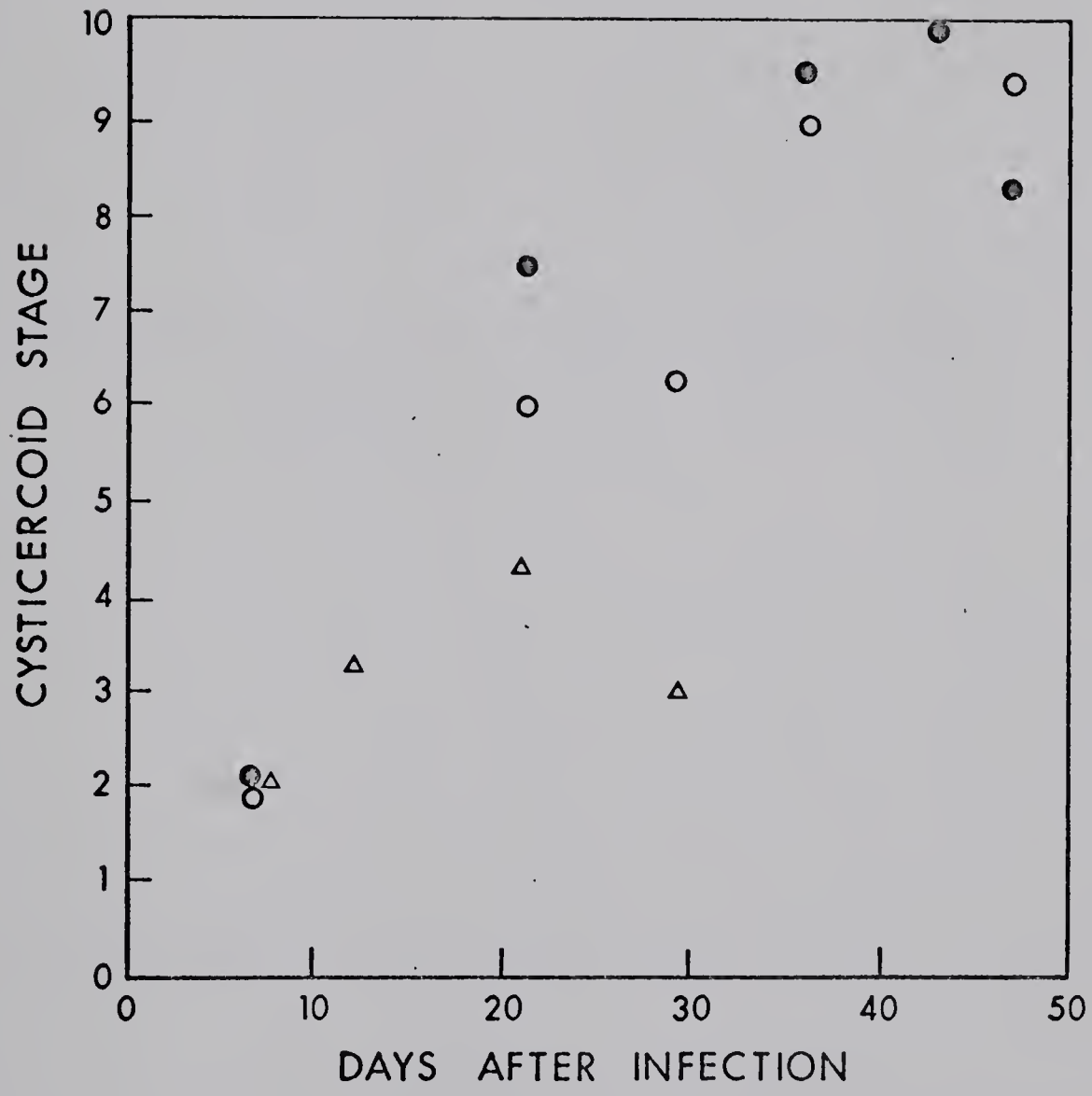
Developmental stage	Minimum number of days after exposure	
	L. skrjabini	L. mathevossianae
Hollow ball of cells	7	11
Elongated body with scolex primordium	12	15
Body differentiated with scolex beginning to withdraw	16	21
Fully developed cysticercoid	36	35

TABLE IV

DIAGNOSTIC CHARACTERS OF THE HYMENOLEPIS SPECIES FOUND

Structure	spiralibursata (5 specimens)	tuvensis (10 specimens)	A (20 specimens)	B (20 specimens)
Length of mature worm	1.5 - 1.9	18 - 25	2.5 - 4.5	4.5 - 6.5
Rostellar hook length	0.028-0.030	0.034-0.037	0.039-0.043	0.049-0.052
Blade length	0.003-0.005	0.012-0.014	0.012-0.015	0.008-0.012
Handle length	0.024-0.026	0.022-0.024	0.025-0.029	0.035-0.041
Length of longest cirrus	?	0.117-0.125	0.101-0.109	0.053-0.061
No. of eggs in uterus	750	20 - 25	750	13 - 19
Diameter of egg	0.033-0.037	0.050-0.058	0.033-0.038	0.033-0.039
Method of shedding of gravid proglottids	singly	singly	singly	as blocks of 9 - 14 segments

Figure 2 Intensity of infection and rate of development of cysticercoids of Lateriporus skrjabini

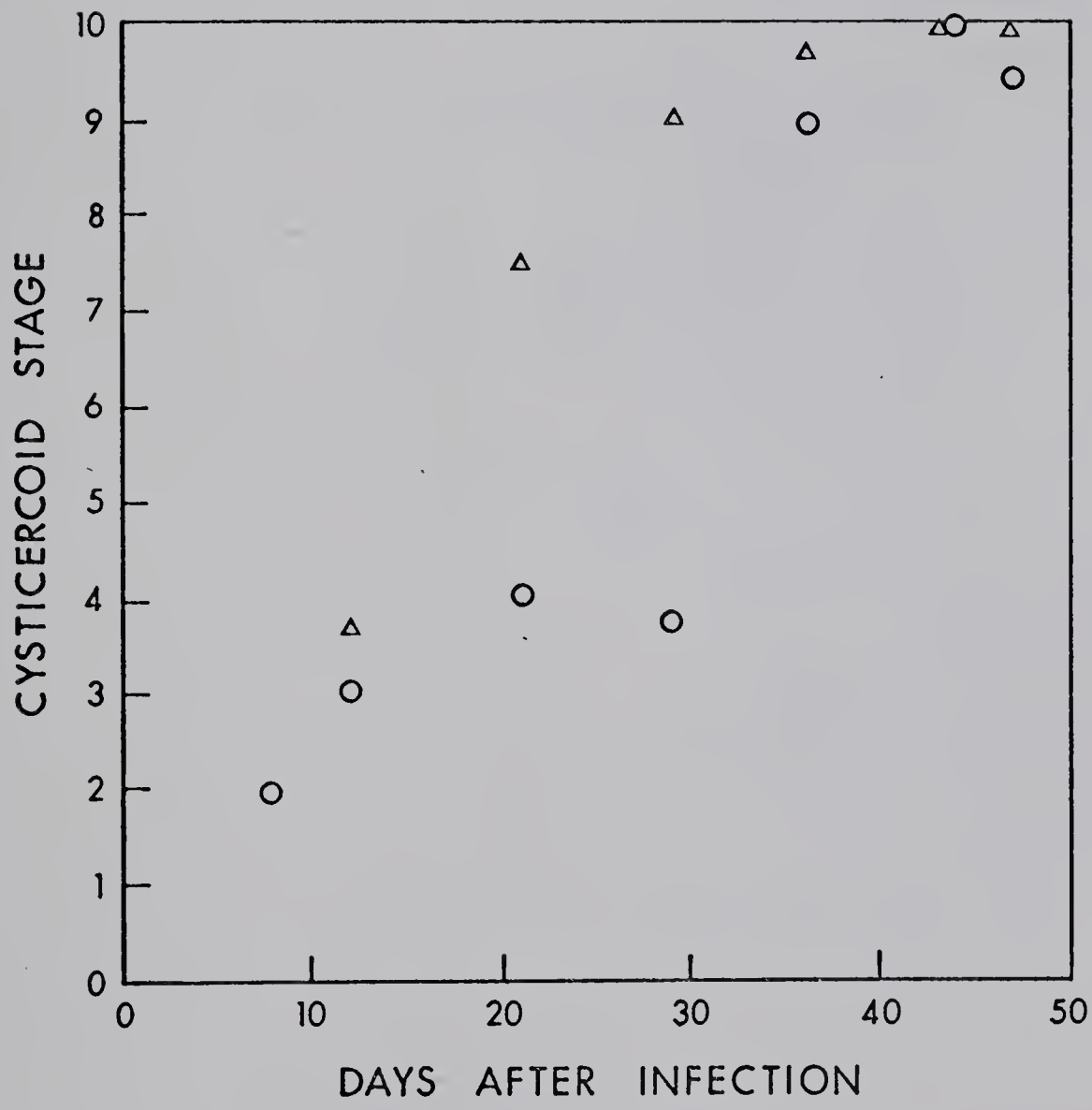


● INTENSITY LESS THAN 20

○ INTENSITY 20-40

△ INTENSITY GREATER THAN 40

Figure 3 Length of the gammarid host and rate of development of cysticercoids of Lateriporus skrjabini



△ GAMMARIDS 10mm AND LONGER

○ GAMMARIDS BELOW 10mm LONG

Figure 4 Hymenolepis tuvensis

A Male proglottid

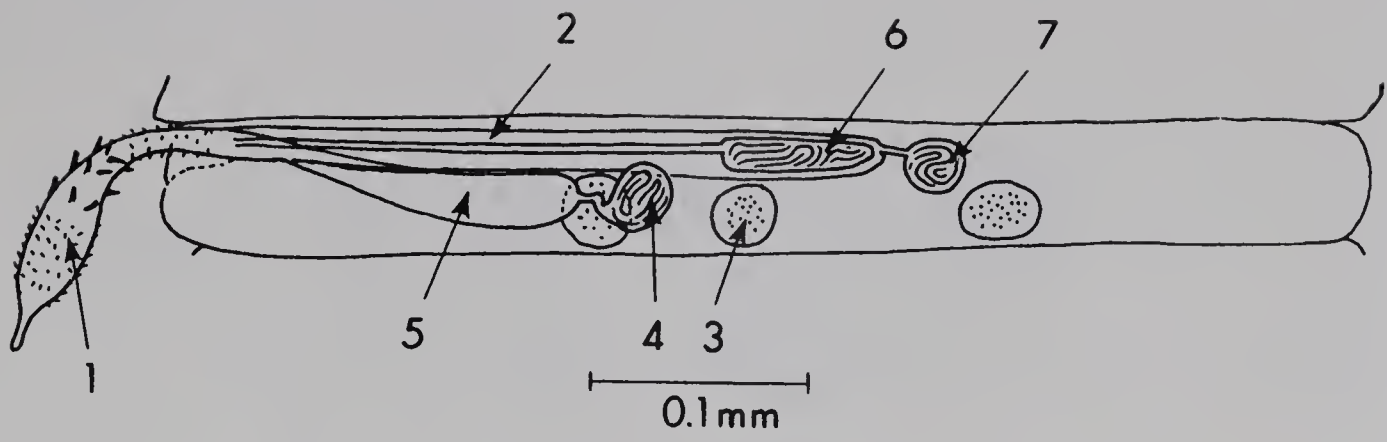
1. Cirrus
2. Cirrus sac
3. Testis
4. Seminal receptaculum
5. Vagina
6. Internal seminal vesicle
7. External seminal vesicle

B Gravid proglottids

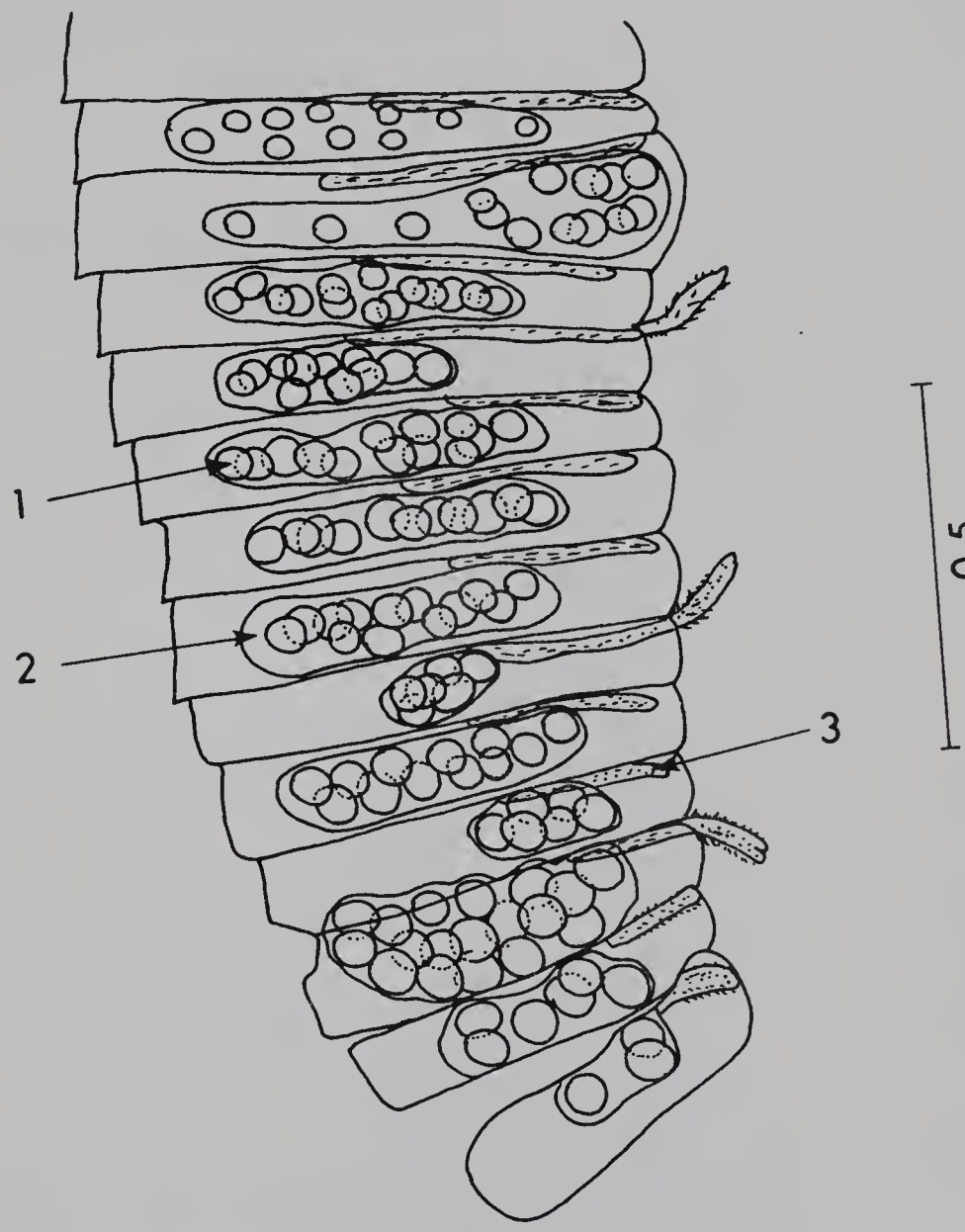
1. Egg
2. Uterus
3. Cirrus sac

C Rostellar hook

A



B



C

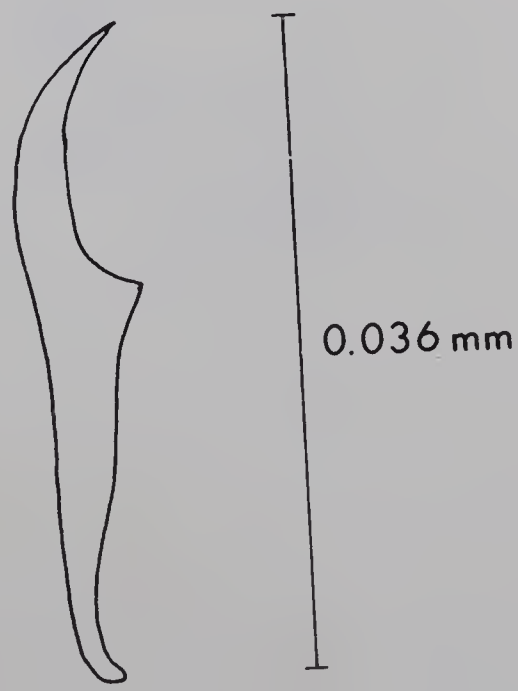


Figure 5 Hymenolepis A

A Male proglottid

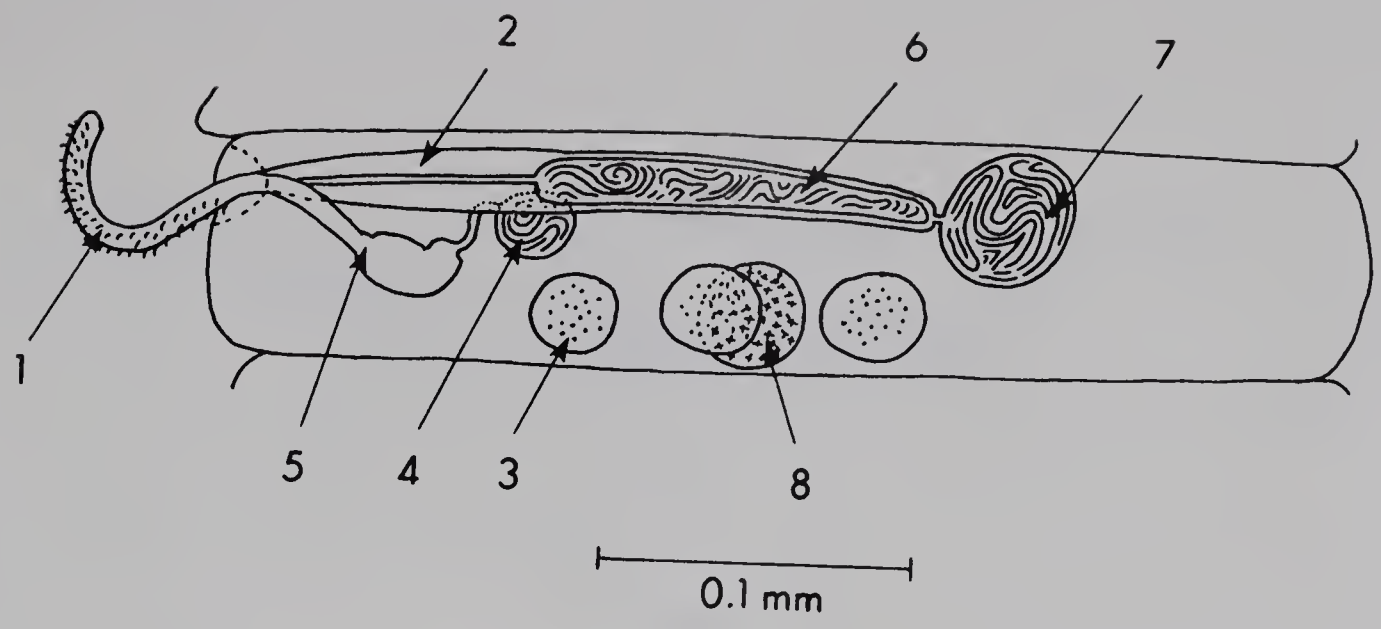
1. Cirrus
2. Cirrus sac
3. Testis
4. Seminal receptaculum
5. Vagina
6. Internal seminal vesicle
7. External seminal vesicle
8. Shell gland

B Gravid proglottids

1. Egg
2. Uterus
3. Cirrus sac

C Rostellar hook

A



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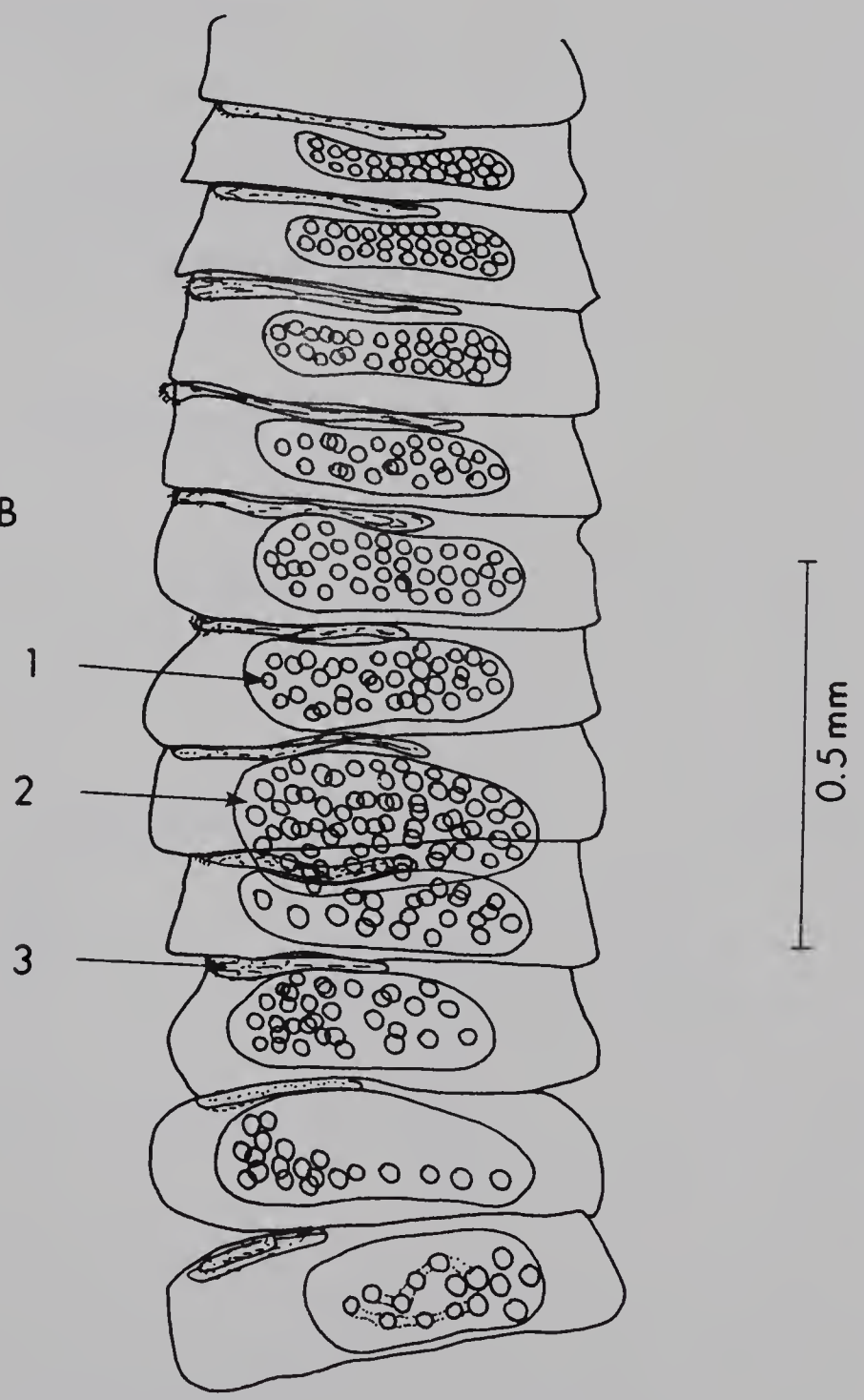

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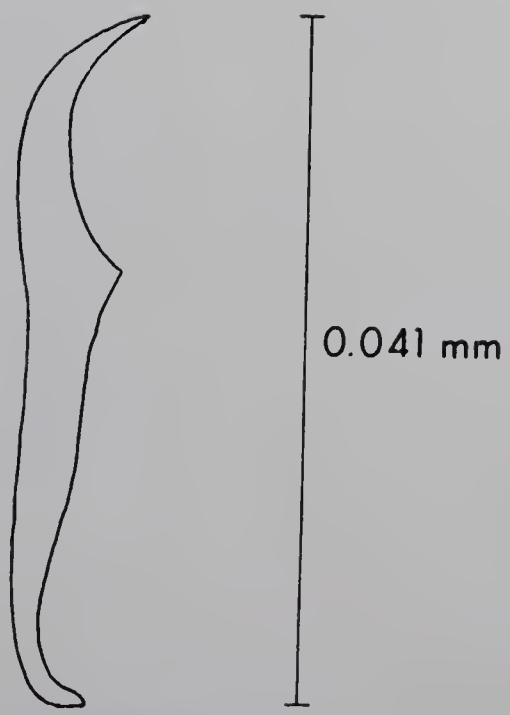


Figure 6 Hymenolepis B

A Male proglottid

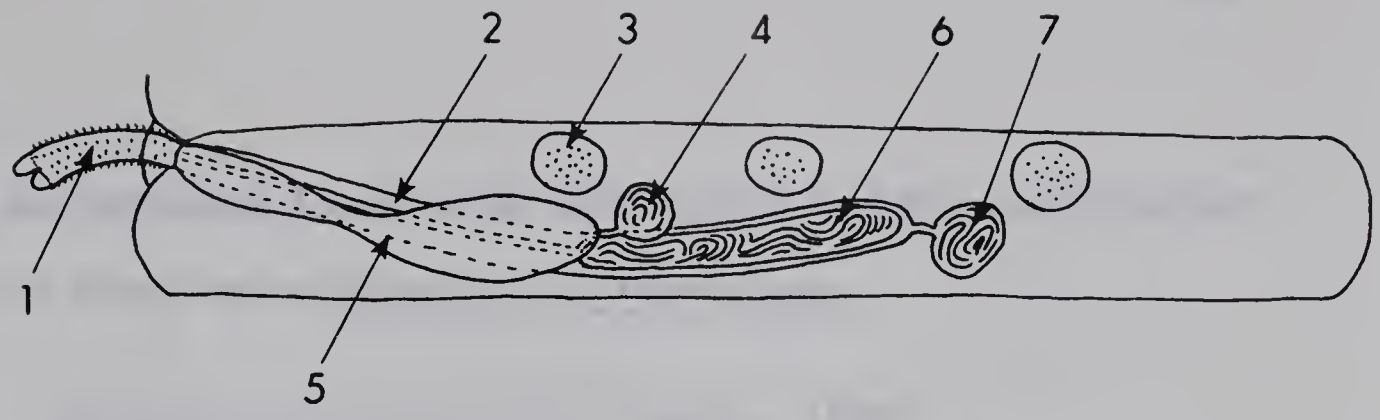
1. Cirrus
2. Cirrus sac
3. Testis
4. Seminal receptaculum
5. Vagina
6. Internal seminal vesicle
7. External seminal vesicle

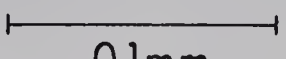
B Gravid proglottid

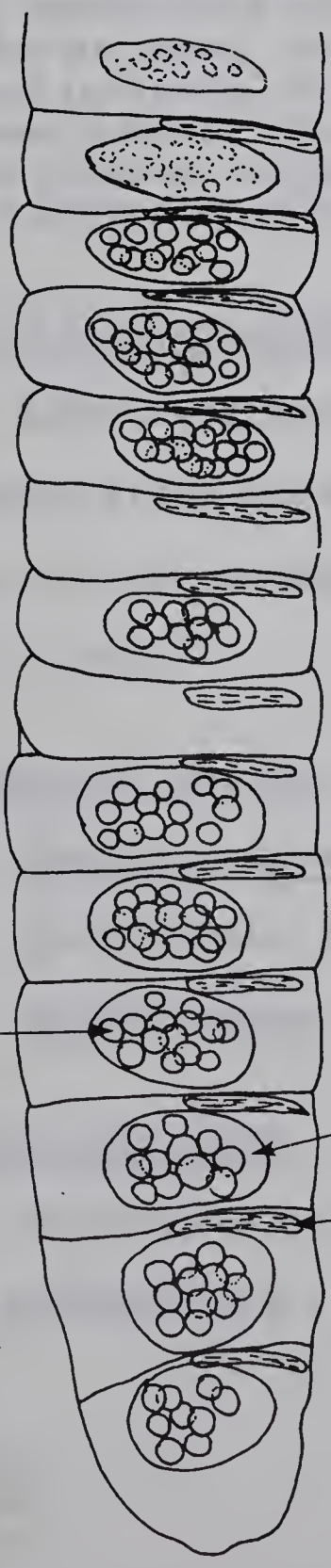
1. Egg
2. Uterus
3. Cirrus sac

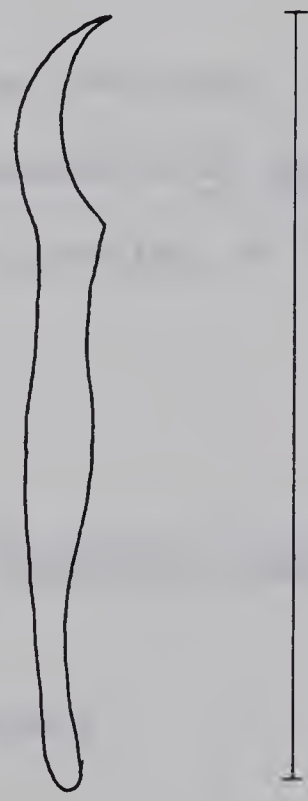
C Rostellar hook

A









NEMATODA

All the juveniles found in the gammarids and the one immature adult raised in a scaup were Streptocara crassicauda.

Streptocara crassicauda (Creplin, 1829)

Description of the juvenile

Excysted juvenile transparent, thin, 3.3 - 4.0 (3·7) long by 0.090 - 0.135 (0.105) wide. Head blunt, with two lips posterior to which is a finely denticulated collarette. Oesophagus 1.000 - 1.200 (1.120) long. Vulva not seen. Anus 0.045 - 0.064 (0.053) from the slightly rounded tail in female, 0.109 from the pointed tail in male. Rudimentary spicule seen in male. (Measurements based on five specimens, one male, four females, fixed in glycerine-alcohol, cleared in glycerine and mounted in glycerine-jelly.)

Development in gammarids

Laboratory infections of gammarids were not attempted. However, Garkavi (1949) traced the development of the parasite in G. lacustris, recording a developmental time, from egg to infective juvenile, of 19 - 25 days at 16 - 20 C.

Host records for juvenile

Gammarus lacustris, Gammarus locusta, Gammarus maeticus (in McDonald, 1965);

Hyalella azteca and Nephelopsis sp. (this study)

Description of the adult

Since it is a well known parasite for which a number of descriptions are available (e.g., Cram, 1927), it will not be described here.

Development in ducks

A single immature female 4.1 long by 0.074 wide was found under the gizzard lining of a laboratory-infected scaup on the fifth day after ingestion. Garkavi (1949) recorded that the parasite reached maturity in the definitive host 9 - 10 days after ingestion.

Host records for adult

Locally: Aechmophorus occidentalis, Podiceps auritus, Podiceps caspicus, Podiceps grisegena, Aythya affinis, Oxyura jamaicensis (mature adults).

Experimentally: Aythya affinis (immature only).

Elsewhere: species of five orders of birds - Anseriformes, Charadriiformes, Galliformes, Gaviiformes, Podicipidformes.

ACANTHOCEPHALA

The cystacanths recovered in this study were all smooth, light to dark orange, lemon-shaped bodies, usually found in the dorsal region of the haemocoel of the gammarids. Experimental infection of laboratory birds with these cystacanths produced adults of three species of Polymorphus (P. contortus, P. marilis and P. paradoxus).

The proboscis hook formula, widely used in acanthocephalan taxonomy, appears not to be a good diagnostic character for these species; they are not separated well by plotting the number of hook rows against the number of hooks per row (Fig. 7). They are, however, separated well by plotting the size of the largest hook against either of the above characters (Fig. 8). They can also be distinguished by size (Table V).

The character that most clearly separates the cystacanths of the three species, however, is the structure of the hind-body wall (Fig. 9). The relative thickness of the cuticle and of the radially striated epidermal layer are equal in P. marilis and P. contortus, both layers being thinner in the latter; however, in P. paradoxus the radially striated epidermal layer is some five to six times thicker than the cuticle. P. contortus may also be distinguished from P. marilis by the marked block-like arrangement of the muscles underlying the striated epidermis in the former.

The adults of the three species can be distinguished from one another on the basis of a combination of characters, some of which, like the proboscis armature, remain unchanged from the cystacanths. Mature adults of P. contortus are smaller, and have smaller eggs, than either those of P. marilis or P. paradoxus and are often highly twisted or

"contorted."

Polymorphus contortus (Bremser, 1821)

Description of the cystacanth (Fig. 10)

Inverted cystacanth (fore-body and proboscis completely invaginated into hind-body) lemon-shaped, 0.570 - 0.625 (0.595) long by 0.440 - 0.500 (0.465) wide, enclosed in a loose capsule that reaches a length of 1.470. (Measurements made on 12 unfixed specimens placed in water for no more than three minutes.)

Total length of everted cystacanth (fore-body and proboscis completely everted from hind-body) 1.665 - 1.750 (1.705). Proboscis symmetrical, cylindrical, 0.285 - 0.305 (0.297) long, 0.140 - 0.150 (0.144) in maximum width, armed with hooks arranged in 15 - 18 (usually 16) rows of 6 - 8 hooks each. Hooks at base of proboscis 0.025 - 0.029 (0.028); at tip 0.031 - 0.035 (0.033). Largest hooks, usually third and fourth from tip of proboscis, 0.040 - 0.044 (0.041) long. The first two or three hooks from base of proboscis generally rootless, remainder with roots that approximate the size of blade. Neck 0.255 - 0.310 (0.280) long, 0.225 - 0.270 (0.245) wide at base, and 0.110 - 0.125 (0.118) wide at junction with proboscis. Two lemnisci present, but not clear. Proboscis sac double walled, 0.435 - 0.570 (0.510) long, extending just into fore-body. Fore-body 0.375 - 0.525 (0.445) long with a mantle of spines, having a maximum length of 0.026 - 0.029 (0.027), extending over all parts. Gonads in posterior of fore-body, rarely in hind-body. Testes two, 0.102 - 0.117 (0.109) long, 0.088 - 0.099 (0.092) wide; ovary diffuse, central;other genital structures rudimentary, present in fore-body and hind-body. Hind-body smooth, lemon-shaped, 0.540 - 0.630 (0.585) long by 0.403 - 0.470 (0.447) wide body wall composed of a distinct outer hyaline cuticle 0.014 - 0.022 (0.017) thick, and an inner, radially striated epidermis 0.014 - 0.025 (0.019) thick. (Measurements based on 20 specimens.)

Development in gammarids

Gammarids were not exposed to infection in the laboratory, accordingly, there is no information on the development of the parasite.

Host records for cystacanth

Gammarus lacustris (this study)

Description of the adult

Body small, 1 - 3 long, often highly twisted, with neck retracted into fore-body. Proboscis armed with 15 - 17 rows of hooks, 6 - 8 hooks in each row. Largest hook 0.040 - 0.047 (0.043) long. Mature eggs 0.080 - 0.110 (0.097) long. (Measurements based on ten specimens.)

Development in ducks

Two males were found in a redhead after a 14 day infection, and females containing mature acanthors were found in a scaup after 33 days.

Host records for adult

Locally: Anas clypeata, Aythya affinis (mature adults); Fulica americana, Anas discors, Anas strepera (immatures only).

Experimentally: Aythya affinis, Aythya americana (mature adults); Anas platyrhynchos, Fulica americana (immatures).

Elsewhere: Anas platyrhynchos, Anas acuta, Anas clypeata, Anas querquedula, Anas strepera, Botaurus stellaris, Lanius collurio.

Polymorphus marilis Van Cleave, 1939

Description of the cystacanth (Fig. 11)

Inverted cystacanth (fore-body and proboscis completely invaginated) lemon-shaped, 0.780 - 0.825 (0.800) long by 0.500 - 0.587 (0.553) wide, enclosed in a loose capsule that reaches a length of 2.050. (Measurements made on 12 unfixed specimens placed in water for no more than three minutes.)

Total length of everted cystacanth (fore-body and proboscis completely everted) 2.294 - 2.442 (2.375). Proboscis symmetrical, slightly bulbous, 0.385 - 0.410 (0.396) long, 0.210 - 0.230 (0.223) in maximum width, armed with hooks arranged in 14 - 17 (usually 16) rows of 6 - 8 hooks each. Hooks at base of proboscis .040 - 0.044 (0.042); at tip 0.050 - 0.056 (0.054). Largest hooks, usually second or third from tip of proboscis, 0.054 - 0.065 (0.060). The first three hooks from base for proboscis generally rootless; remainder with roots that approximate the size of the blade. Neck 0.315 - 0.400 (0.363) long, 0.195 - 0.225 (0.205) wide at base, and 0.105 - 0.135 (0.123) wide at junction with proboscis. Two lemnisci present, but not clear. Proboscis sac, double-walled, 0.560 - 0.735 (0.700) long, extending well into fore-body. Fore-body 0.700 - 0.835 (0.776) long, with a mantle of spines, having a maximum length of 0.020 - 0.023 (0.021), extending over all parts, thinning out on one surface towards junction with hind-body. Gonads in posterior of fore-body, rarely in hind-body. Testes two, 0.120 - 0.151 (0.135) long, 0.082 - 0.094 (0.089) wide; ovary diffuse; other genital structures rudimentary, present in fore-body and hind-body. Hind-body smooth, lemon-shaped, 0.645 - 0.825 (0.735) long by 0.440 - 0.555 (0.495) wide with body wall composed of a distinct outer hyaline cuticle 0.034 - 0.038 (0.036) thick, and an inner radially striated epidermis 0.033 - 0.040 (0.036) thick. (Measurements based on 44 specimens.)

Development in gammarids

The earliest stage observed in this study was the acanthor, recognised by its central embryonic nuclear mass and more peripheral translucent giant nuclei, sometimes observed lying in association with the outer surface of the gut wall in gammarids taken from under the ice during the winter months. These early stages were very small and were generally missed during routine examinations. Sometimes, such acanthors

were "bound" to the gut wall by a membrane of connective tissue, probably the serosa, and associated with a number of smaller host cells, probably haematocytes. Such a stage in development has been described by Crompton (1964) for Polymorphus minutus, when the acanthor, after it had hatched out of the egg membranes and burrowing through the gut wall, came to lie between muscles of the wall and its overlying serosa. It is at this stage that most of the P. marilis may survive the winter (p 89).

The acanthor, at this stage of development, was only about 0.1 mm in length. It grew into a larger, bright orange, more spherical structure, 0.35 mm in diameter, in which the first changes in the embryonic nuclear mass had occurred. This stage, taken by Hynes and Nicholas (1957) to mark the end of the acanthor stage and the beginning of the acanthella stage, corresponded to the first stage of development for which a developmental time (19 days at 23 C) was recorded (Table VI).

The parasite then became distinctly slipper-shaped, the embryonic mass had elongated and had moved into different regions of the acanthella and crenulations appeared on the primordial proboscis which began to evert. This acanthella stage, which is about 1.0 mm in length, was the earliest stage of development recorded in the routine collections of gammarids. The time taken to reach complete eversion of the proboscis was 24 days (Table VI).

Later, the fore-body and posterior end had both invaginated into the hind-body, forming the lemon-shaped cystacanth which lay loosely in a fusiform capsule (Fig. 11a). A minimum of 34 days was taken to reach the fully developed cystacanth. This is longer than that

recorded by Romanovski (1964) for P. minutus in G. lacustris at a comparable temperature (Table VI). Hynes and Nicholas (1957) reported a minimal developmental time of 56 days for P. minutus in Gammarus pulex at 17.0 C. Since Romanovski reported that an increase in temperature from 16.4 C to 24.0 C nearly doubled the rate of development, it is probable that the rate of development of P. marilis in this study would not be very different from that of Hynes and Nicholas' P. minutus at comparable temperatures.

The size of the cystacanth varied according to the number in the gammarid, from 0.780 - 0.825 mm x 0.500 - 0.587 mm in a single infection to 0.680 - 0.730 mm x 0.460 - 0.500 mm in the largest multiple infections observed (15 in a laboratory infection, nine in a natural infection). There appeared to be no correlation between size of cystacanth and size of gammarid.

Cystacanths were invariably found to have their proboscis and fore-body everted in gammarids that had been dead for some time. Occasionally, they were found in this everted condition in live gammarids taken from the lake during the summer. This premature eversion, which involved only the fore-body and proboscis, and not the posterior end and which was always accompanied by a rupture of the capsule, may be a factor contributing to mortality of infected gammarids.

Host records for cystacanth

Gammarus lacustris (this study)

Description of the adult

Body elongate, nearly cylindrical, 9 - 11 long in mature females, 7 - 9 long in mature males. Neck long, slender and retractable. Proboscis armed with 15 - 16 rows of hooks with 2 - 8 hooks in each row; largest hook 0.054 - 0.065 (0.060) long. Mature eggs 0.102 - 0.121 (0.111) long. (Measurements based on 20 specimens from Aythya affinis.)

Development in ducks

In the gut of the host the proboscis and fore-body everted and the cystacanth became attached by its proboscis to the gut wall. The parasites became established in scaup (both in the field and in the laboratory) in a zone from just anterior to the yolk stalk, posteriorly to the entrance of the caecae; this zone is rather sharply defined anteriorly and less so posteriorly.

By day four over half of the parasites had evaginated their posterior ends (Table VII). This apparently took place somewhat earlier in males than in females. In a few of the females, the ovary had begun shedding ovarian balls into the body cavity. On day eight many of the females had a copulation cap covering their posterior ends, and many males had their copulatory bursa everted. The disintegration of the ovary was complete in most females, the body cavity being filled with ovarian balls. On day 10 and 12, immature acanthors were found free in the body cavity and by day 14 mature acanthors were present. The acanthors were infective to gammarids from day 21 onwards (Table IX)..

Nicholas and Hynes (1958) recorded longer developmental times for P. minutus; mature acanthors first appeared on day 19 and

were first infective to gammarids on day 32 (Table VIII).

It is not known whether the acanthors are released from gravid females continuously, as reported by Hyman (1951) and Van Cleave (1953) for many acanthocephalans, or whether they are released only when the gravid female has passed out in the faeces of the duck, as suggested by Nicholas and Hynes (1958) for P. minutus on the evidence that no acanthors were found in the faeces. Unfortunately, faeces were not examined for acanthors in this study. In one scaup in which a population of 27 worms (10 males and 17 females) was established in the laboratory, the first females were passed in the faeces 27 days after infection. The last female was passed on day 63; their mean life span was 42 days.

Host records for adults

Locally:	Aythya affinis, Podiceps grisegena, Oxyura jamaicensis (mature adults); Fulica americana, Anas platyrhynchos (immatures only).
Experimentally:	Aythya affinis, Aythya americana, Anas platyrhynchos domesticus (Pekin strain) (mature adults); Fulica americana, Anas platyrhynchos, Anas platyrhynchos domesticus (Rouin strain) (immatures only); did not become established in Anas discors.
Elsewhere:	Aythya marila, Aythya affinis, Anas platyrhynchos, Tadorna cristata, Bucephala albeola, Bucephala clangula, Fulica atra,

Melanitta sp, Phalacrocorax sp.

Polymorphus paradoxus Connell and Corner, 1957

Description of the cystacanth (Fig. 12)

Inverted cystacanth (fore-body and proboscis completely invaginated into the hind-body) lemon-shaped, 1.050 - 1.350 (1.215) long by 0.765 - 0.870 (0.825) wide, enclosed in a loose capsule that reaches a length of 2.960. (Measurements made on 12 unfixed specimens placed in water for no more than three minutes.)

Total length of everted cystacanth (fore-body and proboscis completely everted from hind-body) 3.230 - 3.560 (3.395). Proboscis symmetrical, slightly bulbous, 0.540 - 0.660 (0.595) long, 0.255 - 0.360 (0.315) in maximum width, armed with hooks arranged in 16 - 19 (usually 17 or 18) rows of 7 - 11 (usually 8 or 9) hooks each. Hooks at base of proboscis 0.049 - 0.055 (0.052), at tip 0.062 - 0.070 (0.067). Largest hooks, usually third and fourth from tip of proboscis, 0.067 - 0.085 (0.079). The first three or four hooks from base of proboscis generally rootless, remainder with roots that approximate the size of the blade. Neck 0.525 - 0.750 (0.635) long, 0.315 - 0.375 (0.347) wide at base and 0.170 - 0.195 (0.183) wide at junction with proboscis. Two lemnisci present but not clear. Proboscis sac double walled, 1.101 - 1.135 (1.112) long, extending well into fore-body. Fore-body 0.750 - 1.055 (0.895) long, with a mantle of spines, having a maximum length of 0.029 - 0.030 (0.029), extending over all parts. Gonads in posterior of fore-body. Testes two, 0.187 - 0.215 (0.196) long, 0.127 - 0.163 (0.148) wide; ovary diffuse; other genital structures rudimentary, present in fore-body and hind-body. Hind-body smooth, lemon-shaped 1.085 - 1.290 (1.165) long by 0.705 - 0.840 (0.784) wide with body wall composed of a distinct outer hyaline cuticle 0.011 - 0.018 (0.015) thick, and an inner, radially striated epidermis 0.062 - 0.108 (0.087) thick. (Measurements based on 17 specimens.)

Development in gammarids

Gammarids were not exposed to infection in the laboratory; therefore, there is no information on the development of the parasite.

Host records for cystacanth

Gammarus lacustris (this study)

Description of the adult

Mature worm 6 - 13 long with somewhat ovoid proboscis armed with 17 - 19 rows of hooks with 7 - 10 hooks in each row. Size of largest hook 0.070 - 0.085 (0.079) long. Mature eggs 0.100 - 0.120 (0.112) long. (Measurements based on 10 specimens.)

Development in ducks

Since no mature worms were raised and only two immatures were found, probably in abnormal hosts, there is no information on the development of the parasite.

Host records for adult

Locally: Aechmophorus occidentalis, Podiceps auritus, Podiceps caspicus, Podiceps grisegena, Melanitta deglandi, Castor canadensis, Ondatra zibethica (mature adults); Fulica americana (immatures only).

Experimentally: Anas strepera, Aythya affinis (immatures only).

TABLE V

COMPARATIVE MEASUREMENTS (in mm) OF THE CYSTACANTHS OF POLYMORPHUS CONTORTUS, P. MARILIS AND P. PARADOXUS

	P. paradoxus (17 specimens)	P. marilis (44 specimens)	P. contortus (20 specimens)
Inverted cystacanth*			
Length	0.570-0.625	0.780-0.825	1.050-1.350
Width	0.440-0.500	0.500-0.587	0.765-0.870
Everted cystacanth#			
Total length	1.665-1.750	2.294-2.442	3.230-3.560
Proboscis length	0.285-0.305	0.385-0.410	0.540-0.666
Proboscis widest width	0.140-0.150	0.210-0.230	0.255-0.360
No. of rows of hooks on proboscis	16 (occ. 15, 17,18)	15-16 (occ. 14, 17)	17-19 (occ. 16)
No. of hooks on each row on proboscis	7-8 (occ. 6)	6-8	7-10 (occ. 11)
Length of longest proboscis hook	0.040-0.044	0.054-0.065	0.067-0.085
Neck length	0.255-0.310	0.315-0.400	0.525-0.750
Neck base width	0.225-0.270	0.195-0.225	0.315-0.375
Proboscis-neck junction width	0.110-0.125	0.105-0.135	0.170-0.195
Proboscis sac length	0.435-0.570	0.560-0.735	1.101-1.135
Fore-body length	0.375-0.525	0.700-0.835	0.750-1.055
Length of spines on fore-body	0.026-0.029	0.020-0.023	0.029-0.030
Hind-body length	0.540-0.630	0.648-0.825	1.085-1.290
Hind-body width	0.403-0.470	0.440-0.555	0.705-0.840
Body wall cuticle thickness	0.014-0.022	0.034-0.038	0.011-0.018
Body wall striated epidermis thickness	0.014-0.025	0.033-0.040	0.062-0.108

*unfixed in temporary water mount

#fixed in A. F. A., cleared in xylene, and mounted in Canada balsam

TABLE VI

DEVELOPMENT OF *POLYMORPHUS MARILIS* AND *P. MINUTUS* IN GAMMARIDS

	Temp. (C)	Minimum days to stage: Acanthor (fully developed)	Acanthella (fully everted proboscis)	Cystacanth
P. marilis (this study)	23	19	24	34
P. minutus Hynes & Nicholas, 1957	17	20	38	56
Romanovsky, 1964	16.4			44
	24.0			25

TABLE VII

MATURITY O F FEMALE POLYMORPHUS MARILIS AFTER VARIOUS PERIODS IN THE DUCK HOST

		Stage of development (Number of females)					
Days after infection	Duck host	Proportion with hind end evaginated	Ovary not shedding Ovarian balls	Ovary shedding Ovarian balls	Ovary broken up, ovarian balls in body cavity	Immature acanthors in body cavity	Mature* acanthors in body cavity
4	Scaup	11/17	8	2	0	0	0
8	Scaup	All	0	1	3	0	0
8	Redhead	All	0	0	1	0	0
10	Scaup	All	0	0	0	2	0
10	Redhead	All	0	0	0	2	0
11	Redhead	All	0	0	0	1	0
12	Scaup	All	0	0	0	9	0
14	Redhead	All	0	0	0	2	8
15	Redhead	All	0	0	0	0	7
16	Redhead	All	0	0	0	0	7
17	Scaup	All	0	0	0	0	2

*Mature acanthors can be distinguished by their rolling pin shape and by the presence of a central mass of nuclei.
Immature acanthors are elliptical and show varying stages of nuclear division, but do not have the central mass of nuclei.

TABLE VIII

RATE OF DEVELOPMENT OF *POLYMORPHUS MARILIS* AND *P. MINUTUS* (FROM NICHOLAS AND HYNES 1958) IN DUCKS

Stage of development of female in duck	Minimum No. of days taken to reach the stage in:	
	P. minutus	*P. marilis*
	Host: domestic duck	Host: scaup
Ovary shedding ovarian balls into body cavity	2	4
Ovary broken up, ovarian balls in body cavity	2	8
Immature acanthors in body cavity	8	10
Mature acanthors in body cavity	19	14
Acanthors infective to gammarid	32	21

TABLE IX

INFECTIVITY TO GAMMARIDS OF ACANTHORS FROM POLYMORPHUS MARILIS AFTER VARIOUS PERIODS IN THE DUCK HOST

Days after infection on which duck was killed	Duck host	Proportion of mature acanthors	Infective to gammarids
11	Redhead	None	No
15	Redhead	Few	No
17	Scaup	Some	No
21	Scaup	About half	Yes
21	Scaup	About half	Yes
24	Redhead	About half	Yes
28	Scaup	Most	Yes
33	Redhead	Most	Yes
34	Scaup	Most	Yes

Figure 7 Hook formulae of cystacanths of Polymorphus contortus, Polymorphus marilis and Polymorphus paradoxus

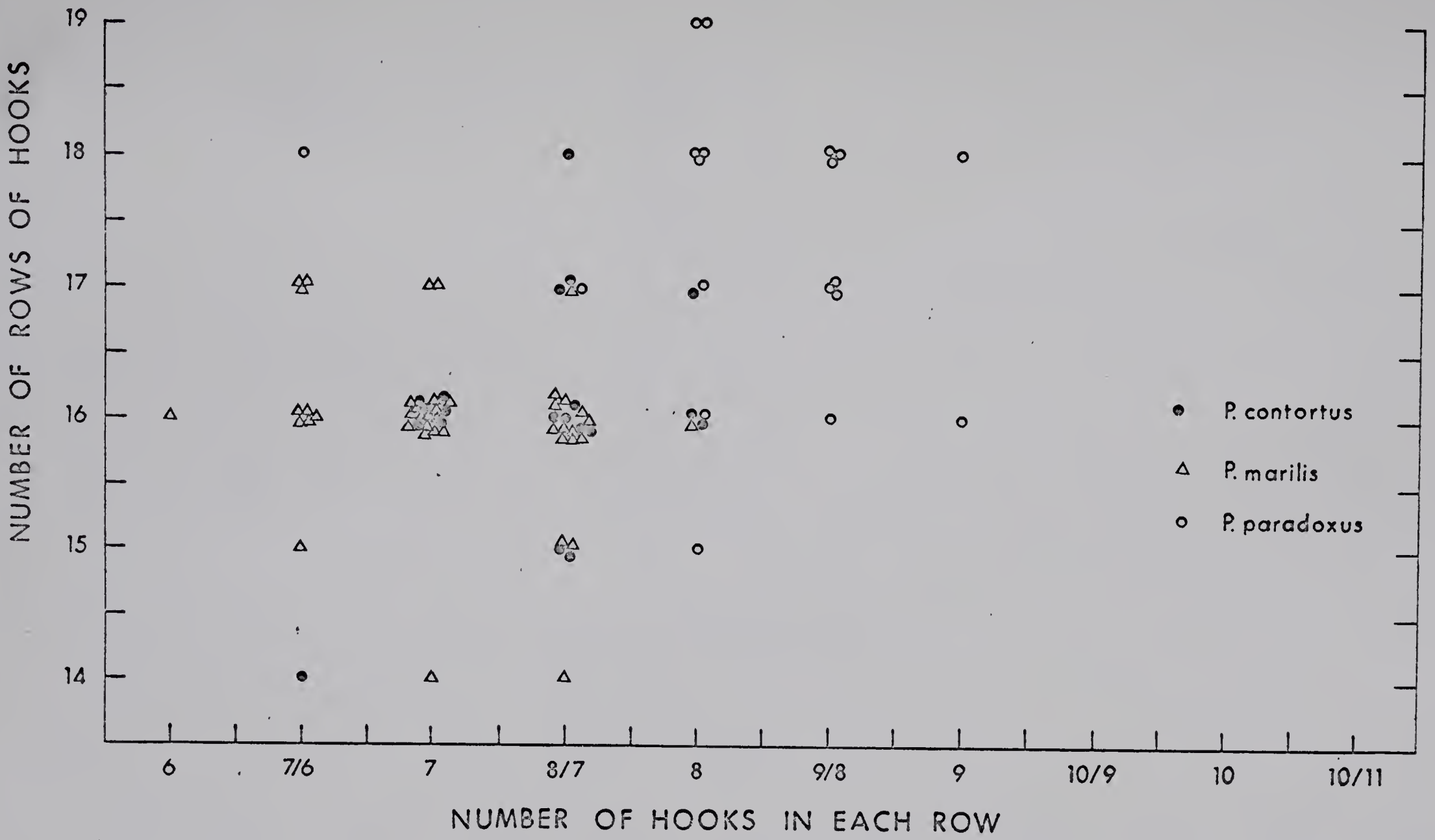

NUMBER OF ROWS OF HOOKS
19
18
17
16
15
14
P. contortus
P. marilis
P. paradoxus
6
7/6
7
8/7
8
9/8
9
10/9
10
10/11
NUMBER OF HOOKS IN EACH ROW

Figure 8 Size of the largest proboscis hook versus the number of hooks in each row for cystacanths of Polymorphus contortus, Polymorphus marilis and Polymorphus paradoxus

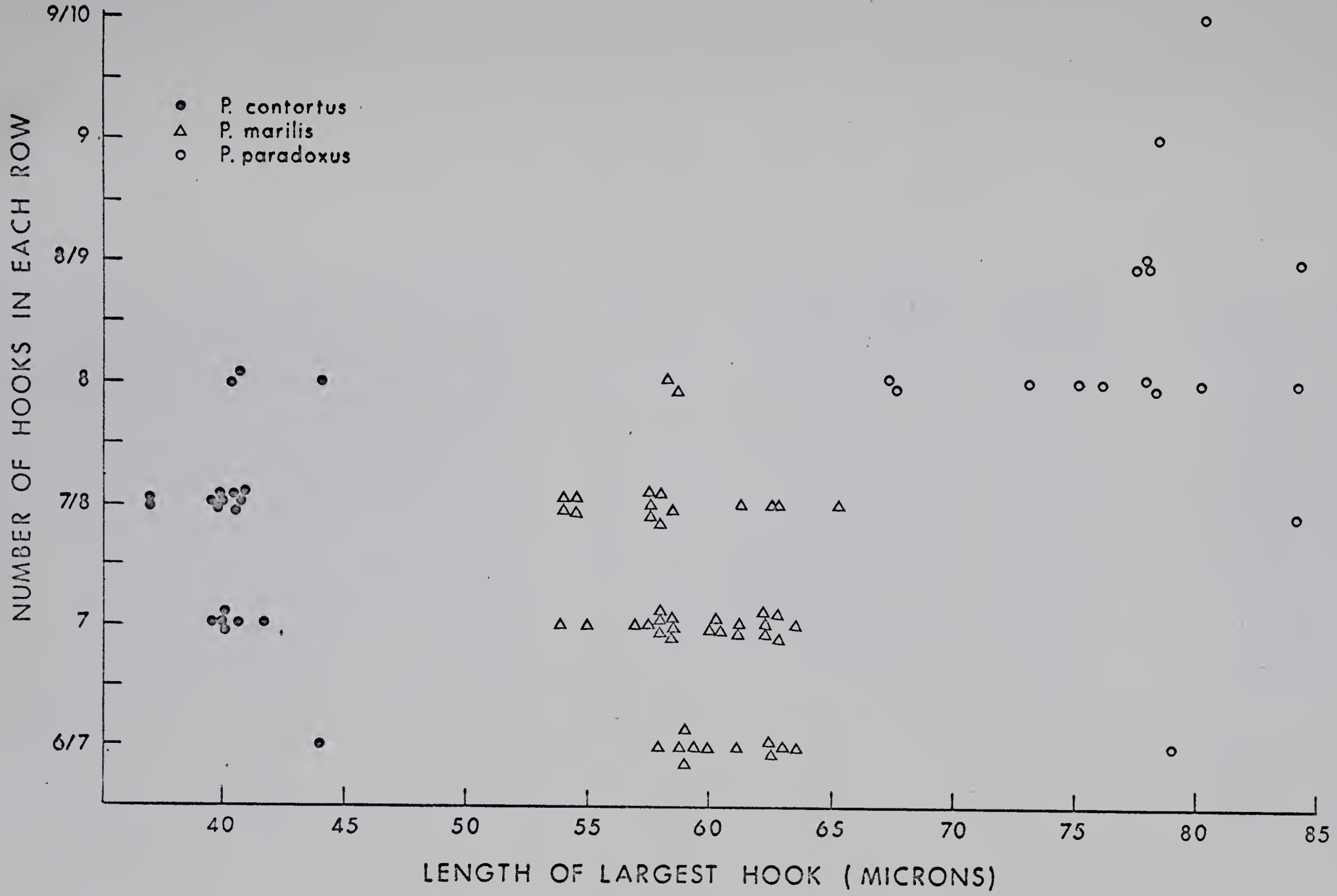
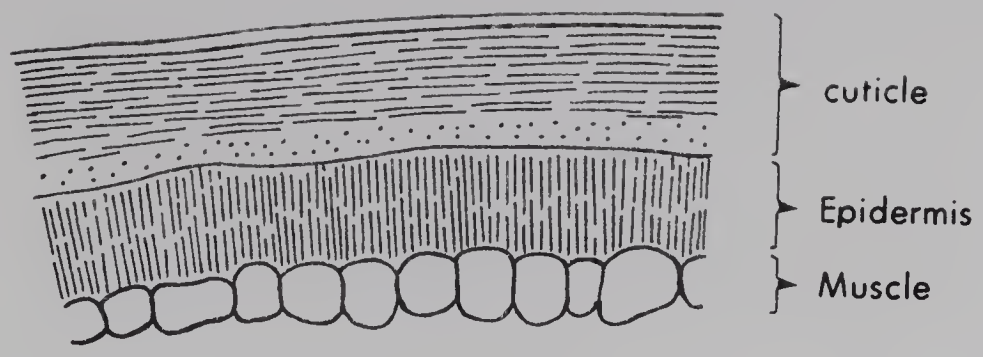
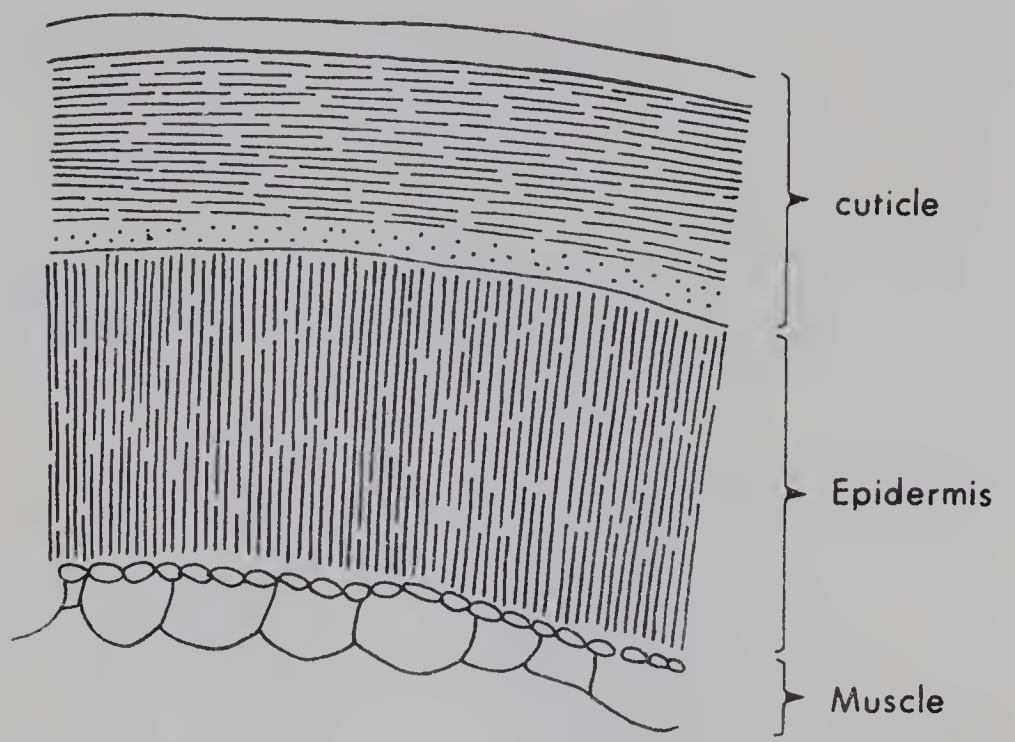

P. contortus
P. marilis
P. paradoxus
NUMBER OF HOOKS IN EACH ROW
9/10
9
8/9
8
7/8
7
6/7
40
45
50
55
60
65
70
75
80
85
LENGTH OF LARGEST HOOK (MICRONS)

Figure 9 Hind-body wall in cystacanths of: A) Polymorphus contortus, B) P. marilis, and C) P. paradoxus

A


cuticle
Epidermis
Muscle

B


cuticle
Epidermis
Muscle
0.025 mm

C

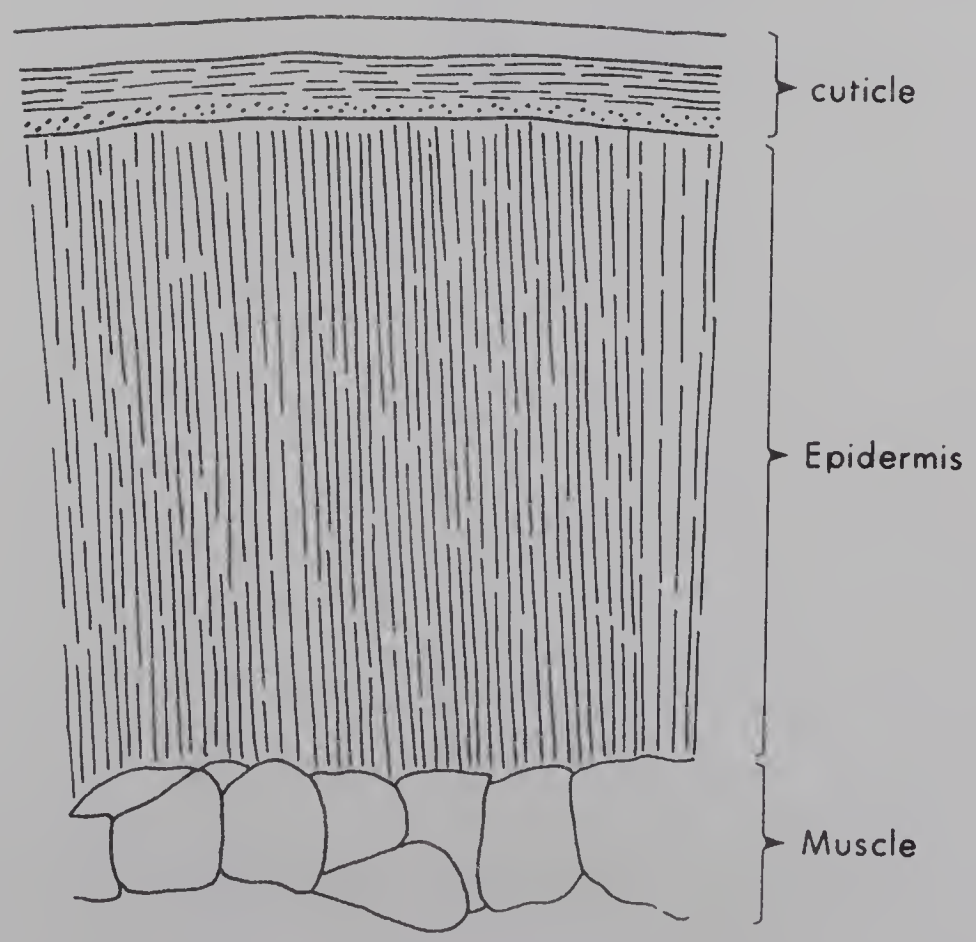

cuticle
Epidermis
Muscle

Figure 10 Polymorphus contortus cystacanth (everted)

1. Proboscis sac
2. Lemniscus
3. Testis
4. Cuticle
5. Radially striated epidermis
6. Muscle blocks
7. Posterior end

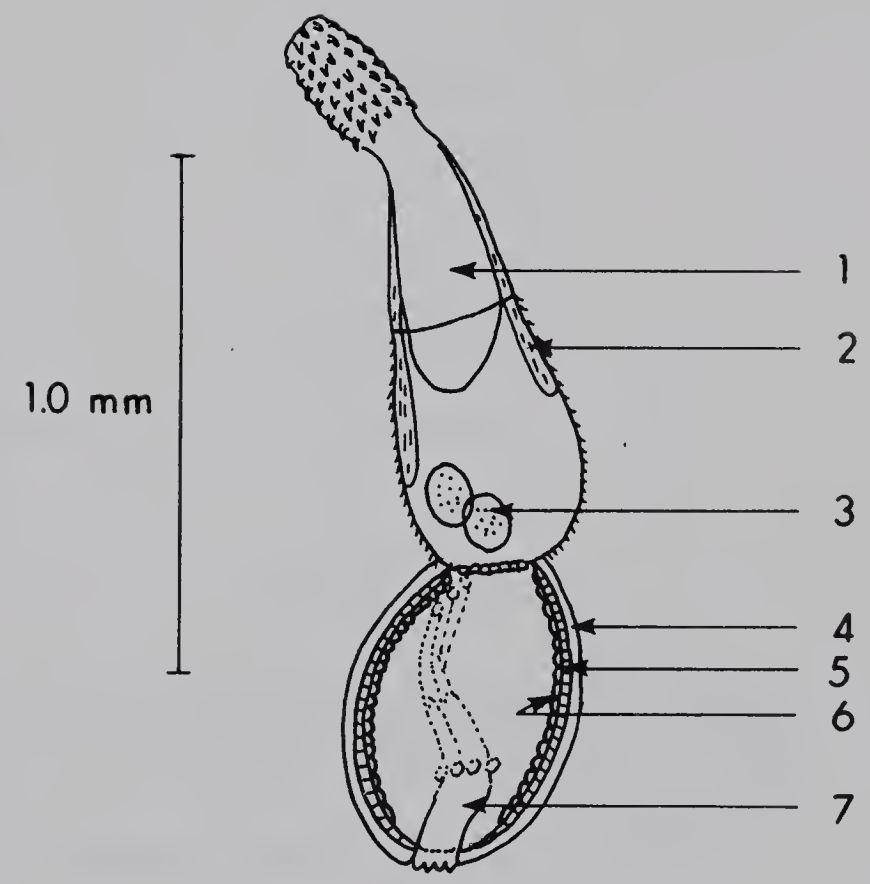

1.0 mm
1
2
3
4
5
6
7

Figure 11 Polymorphus marilis cystacanth

A Inverted cystacanth

1 = capsule

B Everted cystacanth

2 = Proboscis hook

3 = Proboscis sac

4 = Lemniscus

5 = Fore-body hook

6 = Proboscis sheath retractor muscle

7 = Testis

8 = Cement gland

9 = Central ligament

10 = Cuticle

11 = Radially striated epidermis

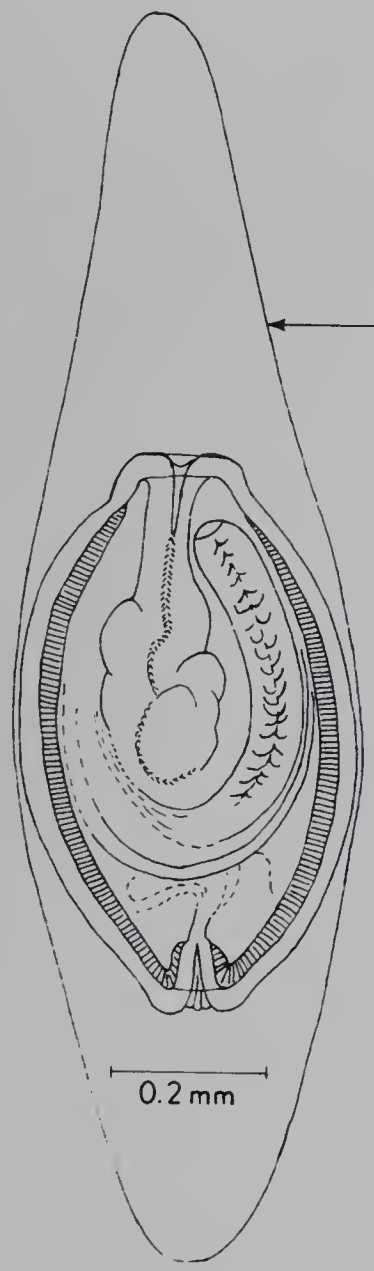
12 = Muscle blocks

13 = Posterior end

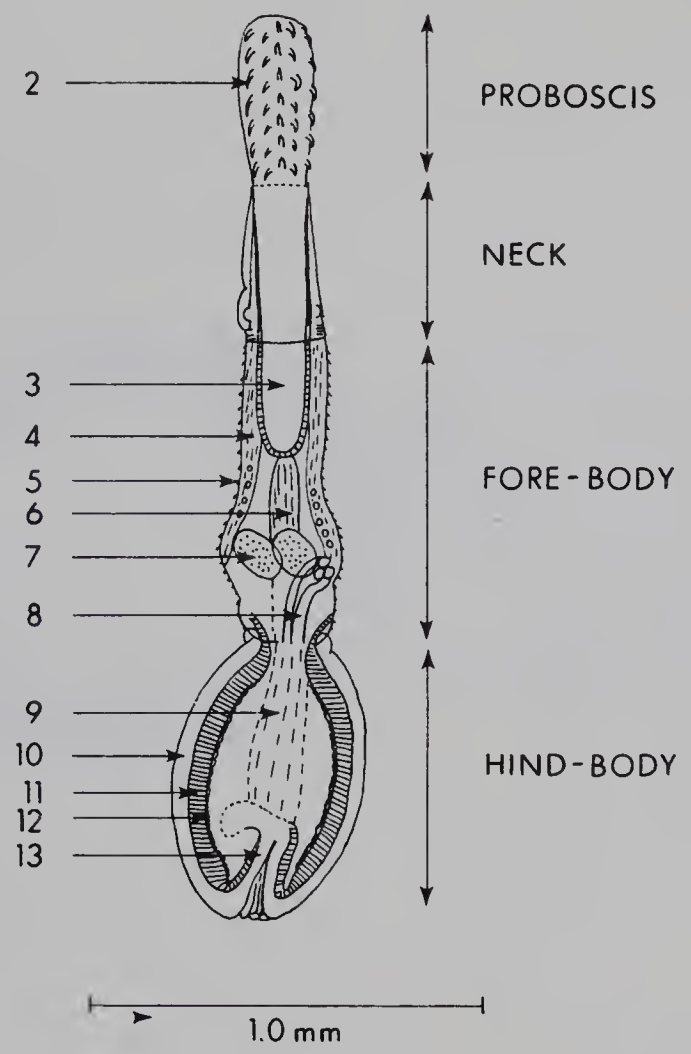
C Proboscis of cystacanth, showing one hook row

14 = Proboscis nucleus

A


1
0.2 mm

B


2
3
4
5
6
7
8
9
10
11
12
13
PROBOSCIS
NECK
FORE-BODY
HIND-BODY
1.0 mm

C

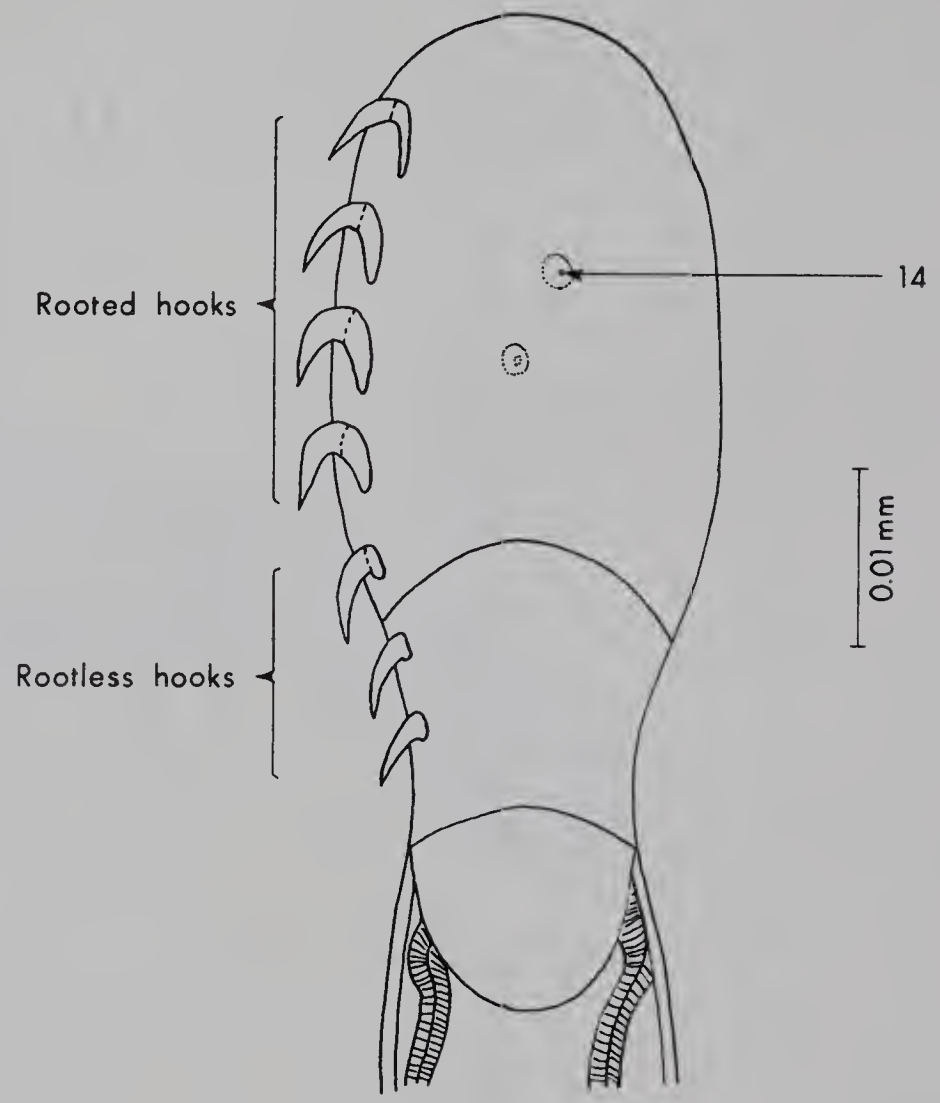

Rooted hooks
Rootless hooks
14
0.01 mm

Figure 12 Polymorphus paradoxus cystacanth (everted)

1 - Proboscis sac

2 - Lemniscus

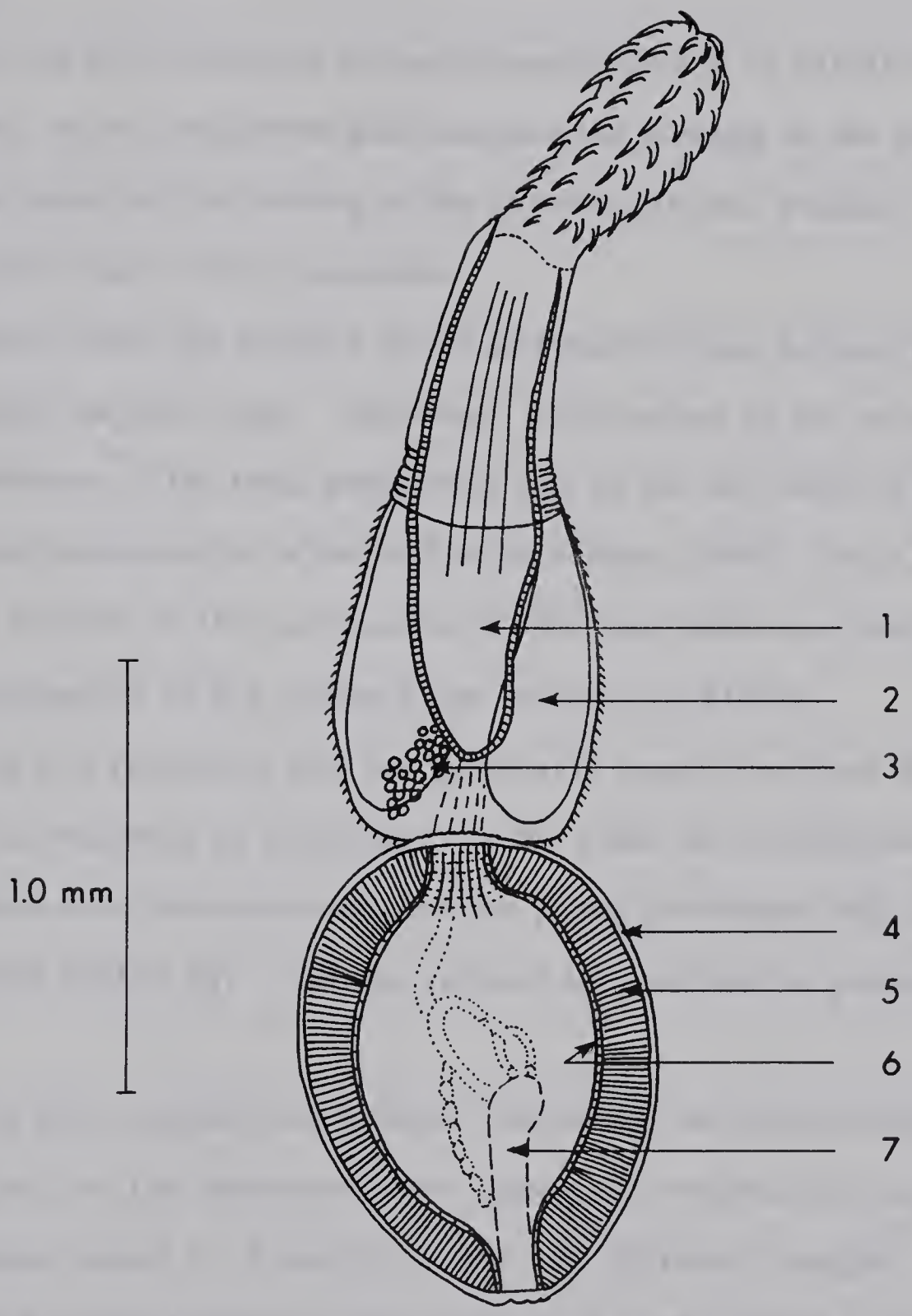
3 - Ovary

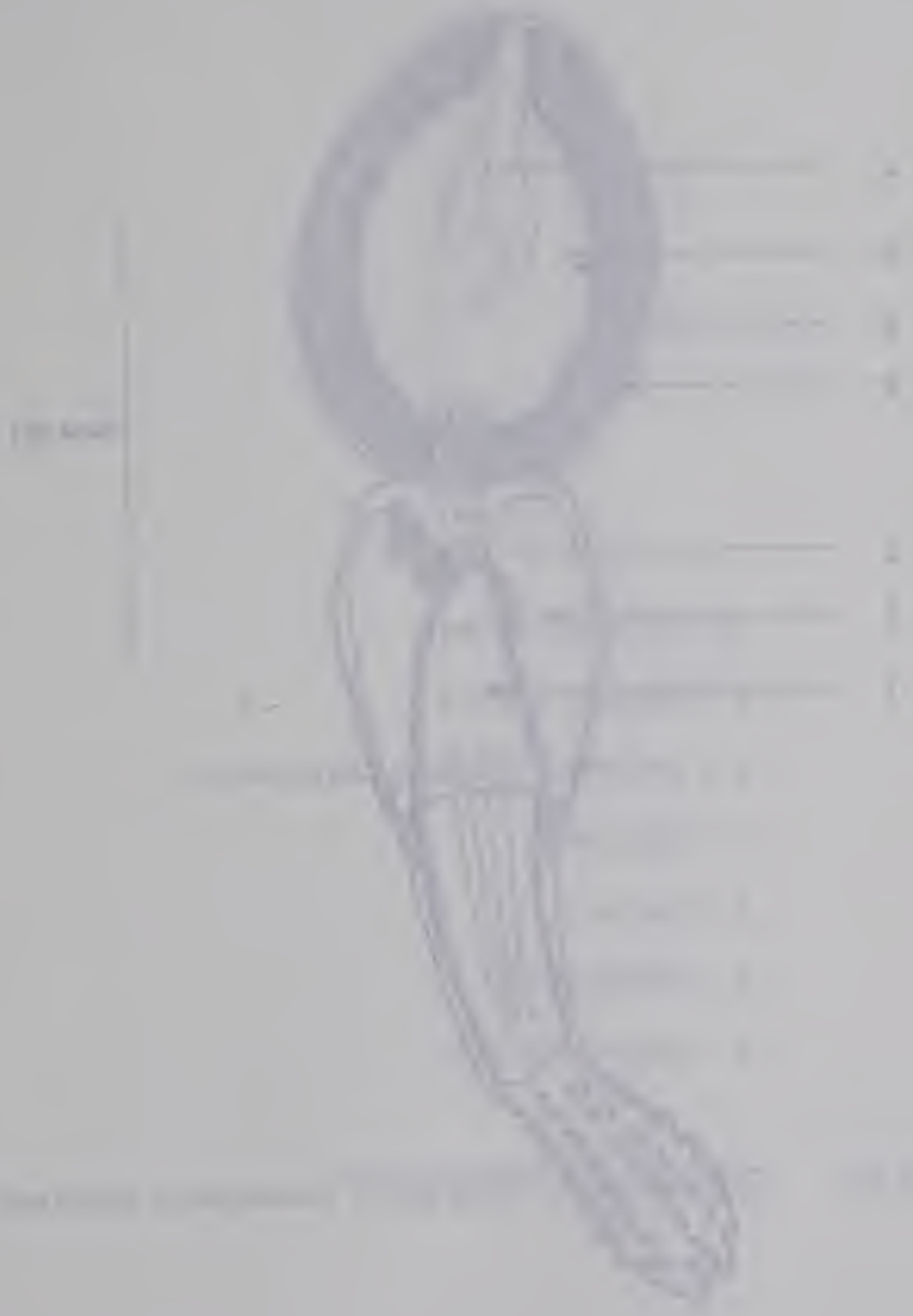
4 - Cuticle

5 - Radially striated epidermis

6 - Muscle blocks

7 - Posterior end


1.0 mm
1
2
3
4
5
6
7



SEASONAL DYNAMICS

The Gammarids

In studies on the ecology of parasite populations it is valuable, if not indispensable, to be acquainted with the general ecology of the hosts. Accordingly, the general life history of the gammarids was studied simultaneously with those of its parasites.

The outline of the life history of the gammarids that follows (Fig. 13) is based largely on this study. However, information on the seasonal variation in abundance of the total population and on the sex ratio of the newborn and young gammarids is derived from Menon (1966), since, in general, the life history of the gammarids of Cooking Lake was similar to that of the gammarids of Big Island Lake, studied by Menon.

The young are recruited into the gammarid population over a two month period from mid-May to mid-July. At the close of recruitment the total population is at its maximum and the young constitute 95% of the total population (Table X). The sex ratio of the newborn is presumably even.

The young grow rapidly and acquire detectable secondary sexual characters (calceoli on the antennae in the males and rudimentary oostegites in the females) when 7 - 8 mm in length. At 10 mm in length, which was reached by the largest males in the last week of July and by the largest females in the second week of August, the calceoli on the males are particularly conspicuous as tiny electric light bulb-like structures and the ovaries in the females become apparent as two dark bands on either side of the mid dorsal line when observed through the

integument. Such individuals from about 10 mm, the time when the ovaries begin to develop, until the onset of the breeding season in the following spring, are referred to as pre-reproductive adults (Menon, 1966).

In the first few months of their life, the young are easily distinguished by length from the parent generation; however, growth is fast in the young and by mid August the largest young are as long as the smallest parents. Gammarids captured from August through May were rather arbitrarily assigned to generations on the basis of break-point lengths (Table XI) determined by the changes in the size class structure of the population and the moulting pattern of the gammarids elucidated by Menon (1966). The break-points between the overlapping size distributions of the two generations are fairly easily determined in August and September but become more difficult to determine in later months. However, since gammarids moult just before freeze up followed by a cessation of moulting until the spring thaw and since a single moult increases the body length of the gammarid by about 1 mm (Menon, 1966) "most probable" break-points may be calculated to distinguish the two generations from October through May.

The abundance of the population just before freeze up is a little less than half of the maximum abundance in mid July. This decrease in abundance is largely due to heavy mortality in the younger generation, which comes to constitute 90% of the total population by the onset of winter. The sex ratio of the pre-reproductive adults at freeze up is about even (Table XII).

The abundance of the gammarid population is further reduced during the winter months, particularly heavy mortality taking place in the month or two preceding the spring thaw due to the prevalence of anoxic conditions in the lake; thus, by the time the thaw comes the population is down to about one third of its maximum level. The younger generation still constituted 90% of the total population when the ice began melting in late April. The fact that the sex ratio was almost even, suggests that the males and females survive equally well over the winter. Some two months before the spring thaw many males and females are found to be swimming around in precopula, with the males holding onto the female by hooking the claws of its first gnathopod to below the front end of the first thoracic segment of the female.

During and just after the spring thaw, males and females moult, then copulate. During copulation, ovulation and external fertilization take place (Menon, 1966). During the first two weeks of May, and coinciding with this reproductive activity, a violent oscillation of the sex ratio took place, first shifting strongly in favour of the males, then in favour of the females. The sudden male mortality was of those gammarids that had completed their part in reproduction (Menon, 1966); the females survive a little longer in order to carry the brood. The population was at its lowest, about one seventh of the maximum level, and consisted of a single generation, the one recruited the previous year, from the first until the third week of May when a new generation of young began to be recruited.

The observations of Menon (1966) suggested that a few females in Big Island Lake may have had two broods during the same summer;

however, no evidence of a second brood was found in this study (Fig. 14). Depending on the size of the females, the number of eggs in a brood varied from 21 - 41 (Menon, 1966). Nearly all females reproduce; a very few small ones never seem to mature.

When the eggs hatch, after an incubation period of three weeks, most of the females die. The small number that survive, together with the surviving males, constitute the post-reproductive adults (Menon, 1966). These are individuals surviving beyond the average life span of thirteen months. After the young are all recruited, the post-reproductive adults constitute 5% of the total population; however, by fall they constitute 10%. Coinciding with the increase in the temperature of the lake water, the proportion of males to females decreases(Fig. 1; Table XII).

Later in the summer, about a week after the females of the younger generation develop into pre-reproductive adults, the ovaries of the post-reproductive females "redevelop" and the females regain their pre-reproductive condition (Fig. 14).

Some of these post-reproductive adults survive the following winter to realize the species' maximum longevity of two years. During the winter they constitute, on the average, a little over 10% of the total population and the ratio of males to females increases appreciably, reversing the trend observed during the summer.

No more post-reproductive adults were recorded in the population after the first week of May; apparently few, if any, live to reproduce a second time.

TABLE X

PERCENT OF THE POPULATION OF GAMMARIDS THAT THE VARIOUS GENERATIONS CONSTITUTE

Date of collection	1964 generation	1965 generation	1966 generation
October 1965	9.9	90.1	
November	13.1	86.9	
December	8.3	91.7	
January 1966	15.5	84.5	
February	10.1	89.9	
March	14.8	85.2	
April 30	9.6	90.4	
May 7	1.4	98.6	
May 17	0	100	
July 6		5.0	95.0
July 20		5.0	95.0
July 29		4.0	96.0
August 10		5.0	95.0
October		10.5	89.5
December		7.0	93.0
March 1967		4.3	95.7

TABLE XI

BREAK-POINT LENGTHS SELECTED TO DIFFERENTIATE BETWEEN GAMMARIDS OF THE YOUNGER AND OLDER GENERATION

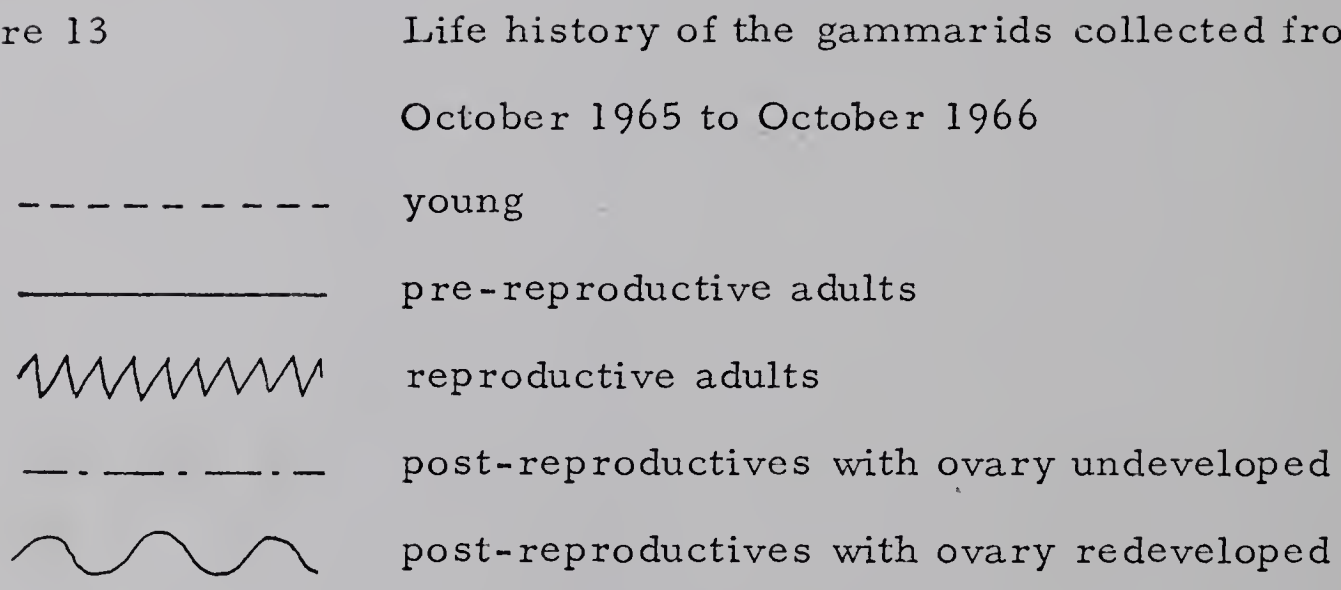
Date of collection	Length (mm.) Male	Female
August 4	11	9
August 10	11	10
August 23	12	10
August 31	12	11
September 14	13	11
September 23	13	12
October	14	12
November	15	13
December	15	13
January	15	13
February	15	13
March	15	13
April 30	16	14
May 7	17	15

TABLE XII

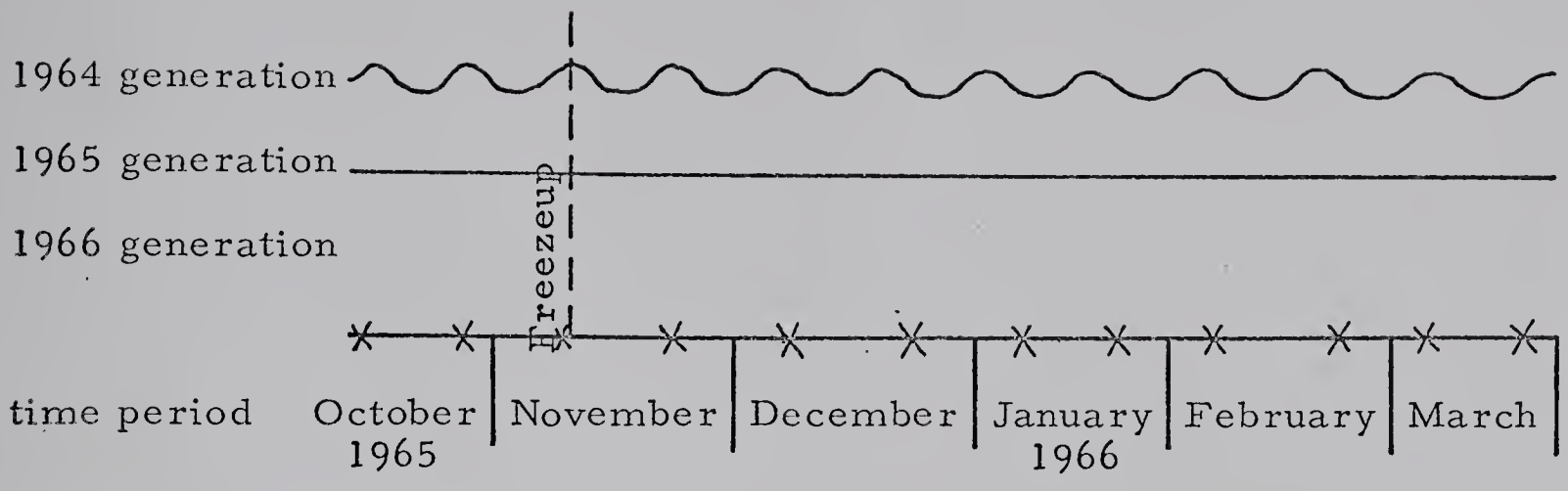
SEASONAL VARIATION IN THE PERCENT OF MALES IN THE THREE GENERATIONS OF GAMMARIDS

Date of collection	1964 generation		1965 generation		1966 generation	
	No. of gammarids	Percent males	No. of gammarids	Percent males	No. of gammarids	Percent males
October 1965	48	50.0	294	35.0		
November	65	66.2	300	54.3		
December	55	61.9	314	42.0		
January 1966	77	71.4	369	63.1		
February	56	69.6	416	50.5		
March	106	64.2	444	53.6		
April 30	29	96.6	268	53.7		
May 7	3	66.7	197	84.3		
May 17			236	37.3		
May 21			330	47.6		
May 31			257	52.9		
June 7	190	52.1				
June 14	100	64.0				
June 20	100	45.0				
June 29	238	50.8				
July 6	213	43.3				
July 11	284	42.3				
July 20	93	23.7				
July 29	298	36.2	8	100.0		
August 4	177	41.2	32	100.0		
August 10	219	41.1	30	100.0		
August 23	150	34.0	50	68.0		
August 31	163	42.3	41	95.1		
September 14	116	51.7	88	78.4		
September 23	41	65.9	147	61.2		
October	46	58.7	393	40.9		
December	14	71.4	163	54.6		
March 1967	8	87.5	180	58.2		

Figure 13 Life history of the gammarids collected from October 1965 to October 1966



x = Date of collection


1964 generation
1965 generation
1966 generation
Freezeup
time period
October 1965
November
December
January 1966
February
March

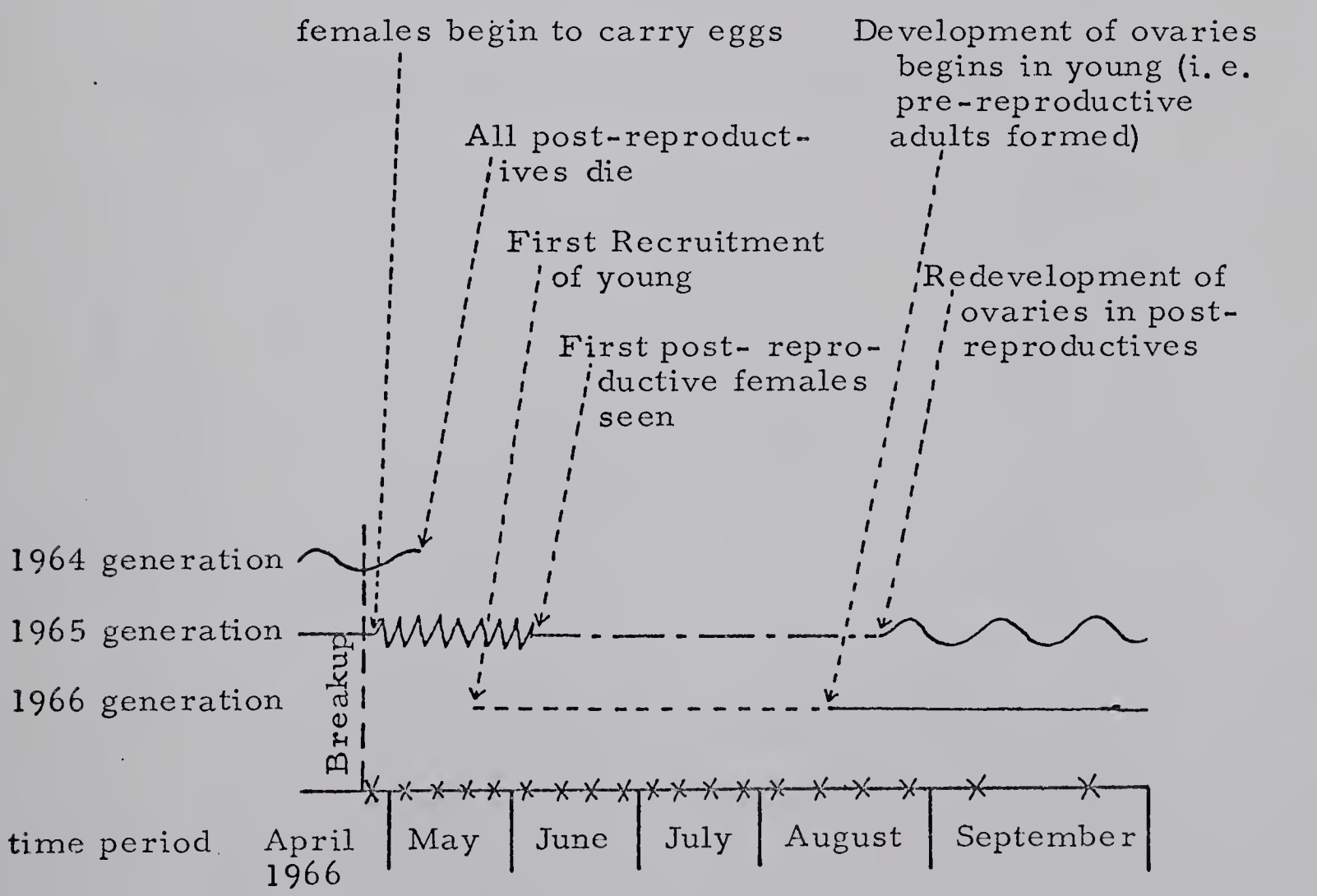
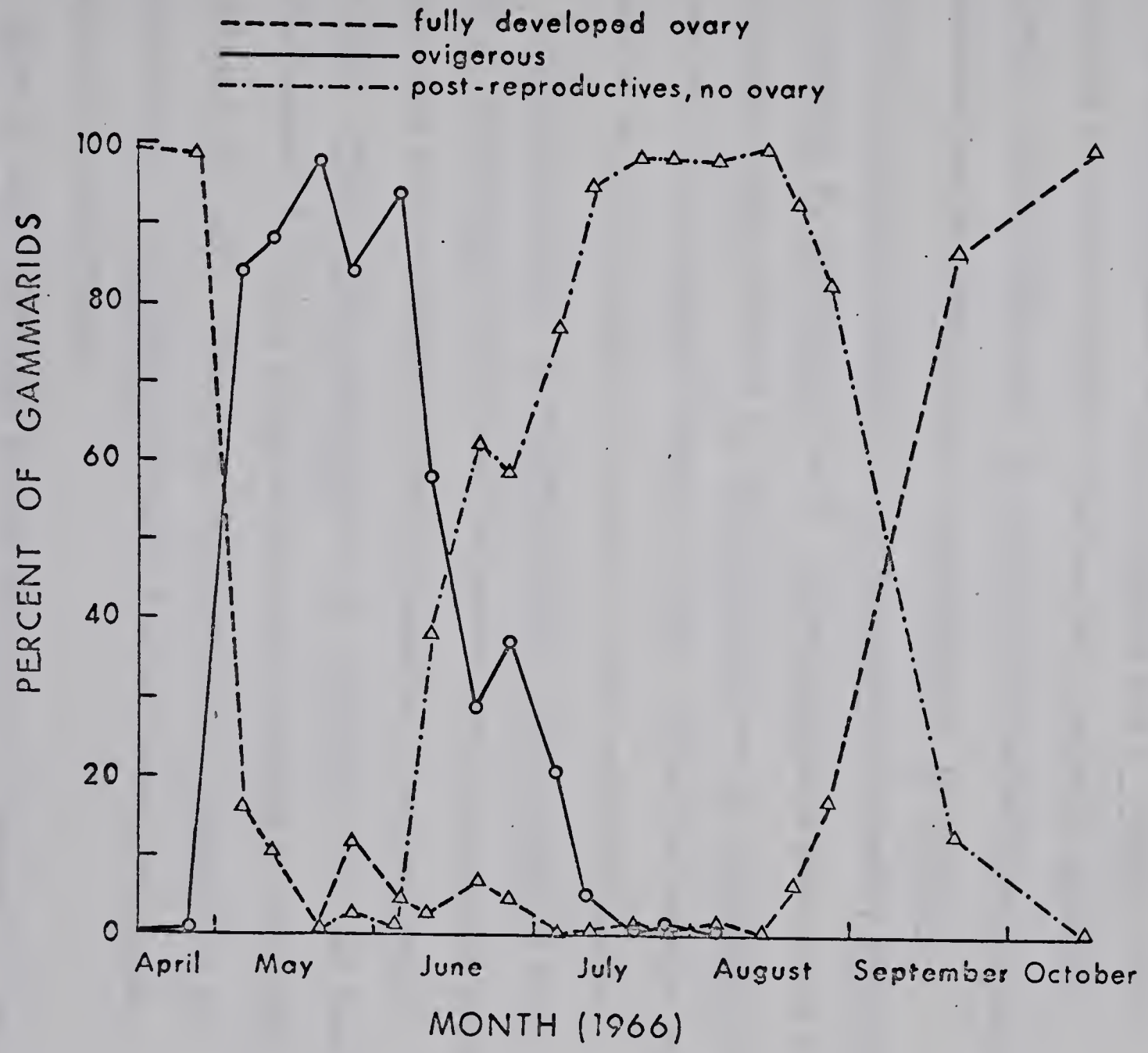

females begin to carry eggs
All post-reproductives die
First Recruitment of young
First post- reproductive females seen
Development of ovaries begins in young (i.e. pre-reproductive adults formed)
Redevelopment of ovaries in post-reproductives
1964 generation
1965 generation
1966 generation
Breakup
time period
April 1966
May
June
July
August
September

Figure 14 Reproductive state of female gammarids of the 1965 generation


fully developed ovary
ovigerous
post-reproductives, no ovary
PERCENT OF GAMMARIDS
100
80
60
40
20
0
April
May
June
July
August
September
October
MONTH (1966)

The Parasites

The moderate to high rates of infection suggest that Gammarus lacustris is the main intermediate host for Lateriporus mathevossianae, L. skrjabini, Hymenolepis B, Polymorphus contortus, P. marilis, P. paradoxus and probably Lateriporus clerci. The last species matures in gulls which do not nest, and have relatively low populations, on Cooking Lake. Of these helminths, only L. skrjabini and P. marilis were encountered frequently enough to discuss their seasonal dynamics separately. On the other hand, G. lacustris is probably not the main intermediate host for Hymenolepis spiralibursata, H. tuvensis, Fimbriaria fasciolaris, Streptocara crassicauda and possibly Hymenolepis A. H. tuvensis, F. fasciolaris and S. crassicauda have been found in the local Hyalella azteca and both H. spiralibursata and F. fasciolaris have been reported from copepods (Jarecka, 1961). These five species were encountered too infrequently to comment on their season dynamics.

Lateriporus clerci, L. mathevossianae, Hymenolepis B and possibly S. crassicauda were found frequently enough during the winter to suggest that they overwinter in the gammarids as mature larvae (Table XIII). Polymorphus contortus and P. paradoxus were not found during the winter, but were found too soon after breakup to allow their development from eggs. They may overwinter in the gammarids as immature larvae. L. skrjabini probably does not overwinter in the gammarids of Cooking Lake.

There is some indication that the behaviour of gammarids infected with cystacanths of P. paradoxus is altered leading to a definite

non-random distribution of the infected hosts. On two occasions, during and immediately after the spring thaw, gammarids clinging to floating pieces of wood were demonstrated to have a much higher incidence of infection with P. paradoxus cystacanths than those swimming around in the water (16.9% and 23% versus 0 and 4% for the two collections respectively). Also, in the samples of gammarids collected during the thaw and maintained in aquaria in the laboratory, the cystacanth-infected gammarids, easily distinguished by the large orange cystacanth in the body cavity visible through the somewhat transparent cuticle, are largely found associated with floating pieces of wood.

TABLE XIII

SEASONAL VARIATION IN EXTENSITY OF INFECTION OF GAMMARIDS (1964 AND 1965 GENERATION AND THE 1966 GENERATION BEGINNING FROM OCTOBER 1966) WITH HELMINTHS

Extensity Infection

Date of collection	No. of Gammarids	Lateriporus				Hymenolepis				Strep-tocara	Polymorphus			
		clerci	mathe-vossianae	skrjabini	Immature	spiraliburs-ata	tuvensis	A	B	crassicauda	contortus	marilis	paradoxus	acanthellae
Oct/65	484		0.2	0.2	0.4			0.4		0.4		3.5		0.8
Nov	498	0.1	0.2		0.4				0.4			3.4		0.6
Dec	660		1.1									2.1		0.5
Jan/66	497				0.2				0.4			1.4		0.8
Feb	554		0.2						0.4			1.8		0.9
Mar	714	0.1	0.1		0.1					0.1		1.8		0.3
Apr 30	303	0.3	0.3				0.3		0.3			1.7	4.0	
May 7	215				3.7				0.9		0.5	3.3	0.5	1.9
May 17	313	0.6			1.9			0.6	0.6	0.3	0.6	4.5	2.6	1.3
May 21	383				2.3				0.3		0.3	7.3	0.5	2.1
May 31	338		0.3		1.8		0.3	0.9	0.6			4.1		9.2
Jun 7	198		1.5	9.1	0.5						1.0	8.6	0.5	14.1
Jun 14	100		2.0	16.0					3.0			13.0		13.0
Jun 20	100		3.0	16.0	1.0			1.0	1.0			13.0		23.0
Jun 29	238		1.3	10.9			0.4	0.8	0.8		1.7	29.0		14.7
Jul 6	102	1.0	3.9	21.6				1.0			2.0	41.0	1.0	13.7
Jul 11	284			14.1				0.4	1.1		6.0	33.1	1.1	2.1
Jul 20	93		1.1	4.3				1.1			4.3	50.5		1.1
Jul 29	196	1.5	1.5	2.1	1.9				0.5		4.6	33.2	4.6	2.0
Aug 4	177			18.6	1.0	0.6			0.6		2.8	50.3	2.8	0.6
Aug 10	219	0.9	4.1	16.0	0.9				1.4	0.5	3.2	49.5	4.6	0.5
Aug 23	149	0.7	3.4	20.0	0.7			0.7	1.3		1.3	62.0	0.7	
Aug 31	163		1.2	6.1	0.6				0.6		0.6	46.7	0.6	
Sept 14	116			2.6					0.9			21.6		
Sept 23	41			4.9								29.3		2.4
Oct	594		0.2	0.2	0.2				0.3			6.4	0.2	2.8
Dec	200			1.0								6.5		2.0
Mar/67	188											2.7	0.5	1.1

Lateriporus skrjabini

Only an occasional mature cysticercoid of L. skrjabini was recorded in the collections of gammarids made during the winter, not enough to provide an effective nucleus of infection for the birds in the spring. Immature Lateriporus cysticercoids found during the winter were probably L. clerci or L. mathevossianae, mature cysticercoids of which were found periodically throughout the winter.

There was a marked rise in the frequency of immature cysticercoids of Lateriporus shortly after the spring breakup. Some of these must have been L. skrjabini, mature cysticercoids of which appeared in early June and rapidly rose to a peak extensity in early July (Fig. 15). A trough of low abundance in the second half of July separated this peak from a second peak in the first three weeks of August; the latter was followed by a rapid decline in abundance.

This pattern in abundance of the adults of L. skrjabini in scaup in the summer (Fig. 16) is also bimodal (Graham, 1966), with high populations in scaup following, and evidently derived from, highs in the gammarids. The information on the developmental times of the cysticercoids (36 days at 23 C) and the adults(8 - 9 day prepatent period) suggest that the helminths making up the second peak were a second generation derived from those of the first peak.

The rise in abundance to a peak is readily explained, in both hosts, by the abundance of infective material available to them. The rapid decline in abundance, however, is not so readily explained. Both a reduction in the rate of infection (due to a reduced availability of

infective material) and a rapid elimination of the existing infections are required. Laboratory experiments demonstrated that the life span of adult L. skrjabini in scaup and redheads is short, only 24 - 25 days. This brief life span, and the low frequency of mature cysticercoids in gammarids at the time, readily explain the rapid decline in scaup.

The rapid decline in the numbers of adult worms in scaup undoubtedly reduces the availability of material infective to gammarids, but there is no evidence to suggest that the cysticercoids, per se, have a short life span. However, observations of laboratory infections suggest that gammarids infected with L. skrjabini die soon after the parasite reaches the mature cysticercoid stage. Mortality of the infected gammarids could help explain the decline in abundance of cysticercoids at the end of the peaks.

Infected young gammarids (1966 generation) were observed only occasionally (Table XIV). Since young were readily infected in the laboratory, and there seems little reason to believe they were not exposed to infection in the lake, the infected individuals probably have short life spans. Consequently, the young appear to contribute very little to the parasite population during the summer of their recruitment.

Both the number of cysticercoids in the gammarids and the number of adults in the scaup are greatly reduced in September and October. An occasional cysticercoid is probably picked up by the scaup in these two months, as witnessed by the presence of a few immature adults (Graham, 1966).

There are two aspects of the population ecology of L. skrjabini left unresolved: 1) the source of the eggs that produce the cysticercoids which appear in the gammarids shortly after breakup; and 2) the part played by the adults of the second peak in scaup, which appear to leave no offspring.

Only two of over a thousand gammarids collected a month before breakup or very early in breakup (probably before many ducks had moved into the lake) were found to harbour L. skrjabini when autopsied immediately, or after maintaining them at laboratory temperatures for two to four weeks. It would appear, then, that overwintering gammarids are not sufficiently infected to account for the spring infections in ducks, and that the eggs do not come from worms in birds of the previous summer, unless the gammarids suddenly become infected with them after the last collection was made. There is nothing to support such a suggestion.

Autopsies of ducks, particularly scaup, arriving at their summer breeding ground around Edmonton reveal a few mature and some immature L. skrjabini, suggestive of recent infections (Graham, 1966; Graham and Podesta, 1967 - personal communication). These worms could provide infective eggs as soon as the ice melts in the spring, but it is questionable whether the 29 - 37 days between breakup and the appearance of large numbers of cysticercoids in the gammarids is long enough for the development of the cysticercoid at the low May water temperatures (Fig. 1). In the laboratory, at 23 C, this process required 36 days. However, as discussed earlier, the very high

intensities of infection in the laboratory gammarids could have slowed the rate of development of the parasite appreciably, so that less time would be required in less intense infections.

If birds feeding on the lakes as soon as there is sufficient exposed water do provide the source of eggs which produce the initial appearance of cysticercoids in the spring, the adults in scaup in late August apparently play no part in the population ecology of L. skrjabini in Cooking Lake. However, an interesting problem is raised here, namely, from where and when do these early spring ducks acquire their infections?

There are apparently no records of L. skrjabini from the wintering grounds or migration routes in North America (McDonald, 1965); consequently, it is probable that the worms overwintered, and were acquired, in this general region. Cooking Lake and other lakes open considerably later than the small sloughs, many of which have flourishing gammarid populations. The prepatent period (8 - 9 days in scaup and redheads) is sufficiently short to allow the ducks ample time to acquire some mature worms before moving onto Cooking Lake, since they often arrive in the general area two to three weeks before the first clear water is available on Cooking Lake.

There is a considerable movement of ducks, including scaup, around the general area in August and September prior to southward migration. It may be that eggs passed out by the ducks during the fall produce infections in gammarids in some other bodies of water, and that the infected gammarids do overwinter, providing a source of

infection to the first birds arriving in the spring. There are no data to support this suggestion, however.

TABLE XIV

EXTENSITY OF LATERIPORUS SKRJABINI IN THE LARGER SIZE CLASSES OF YOUNG GAMMARIDS (1966 GENERATION)

Date of collection	Size class (mm.)	No. of gammarids	No. of cysticercoids
June 29	4, 5, 6	75	0
July 6	5, 6, 7, 8	86	0
July 20	7, 8, 9	62	0
July 29	9, 10	41	1
August 4	9, 10, 11	250	0
August 10	10, 11	30	0
August 23	10, 11, 12	50	2
August 31	10, 11, 12	41	0
September 14	10, 11, 12, 13	88	1
September 23	10, 11, 12, 13	147	1
October	6, 7, 8, 9, 10, 11, 12, 13	548	1
December	6 - 16	186	0

Figure 15 Seasonal variation in extensity of cysticercoids of Lateriporus skrjabini in the 1965 generation of gammarids

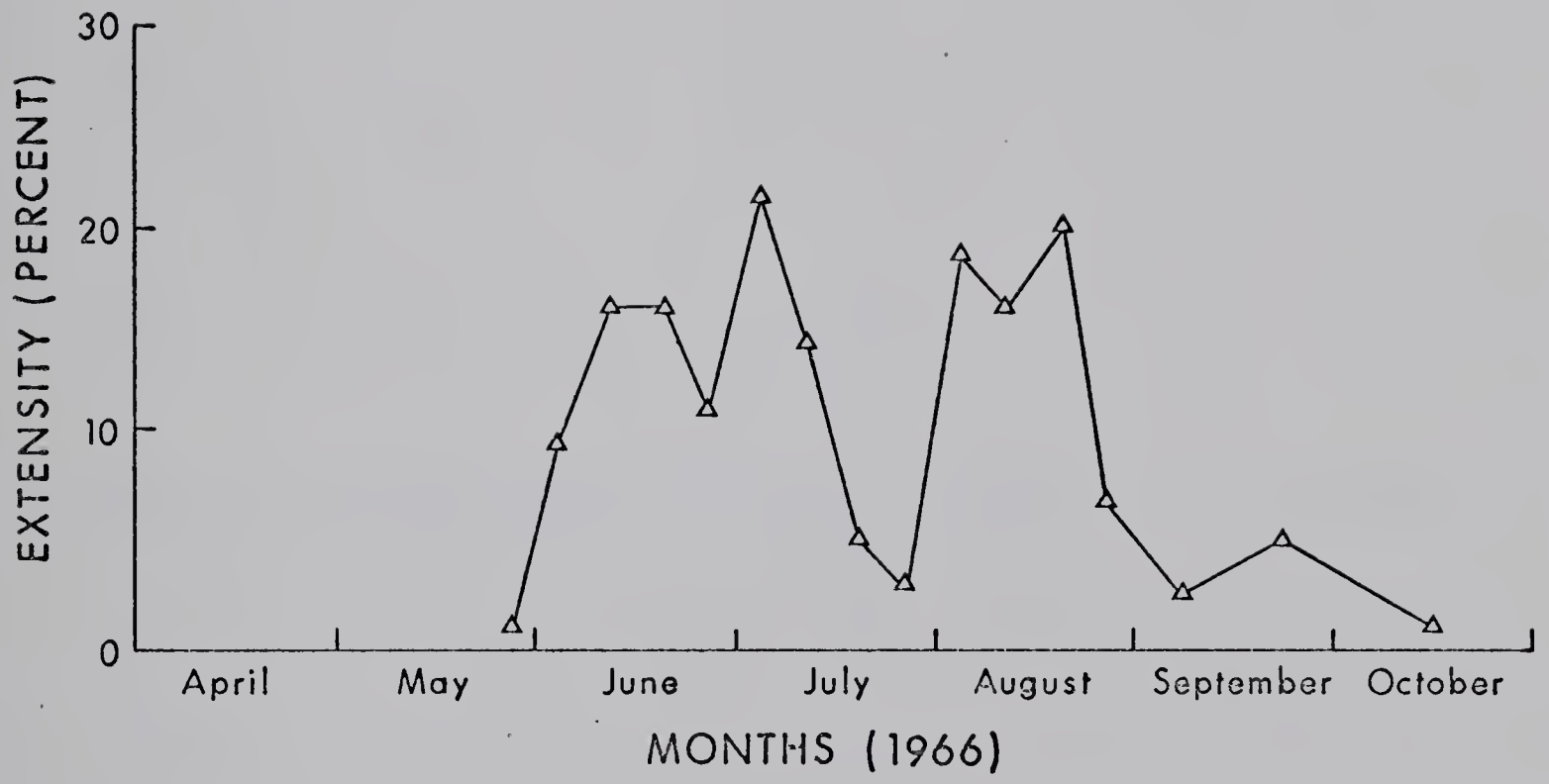
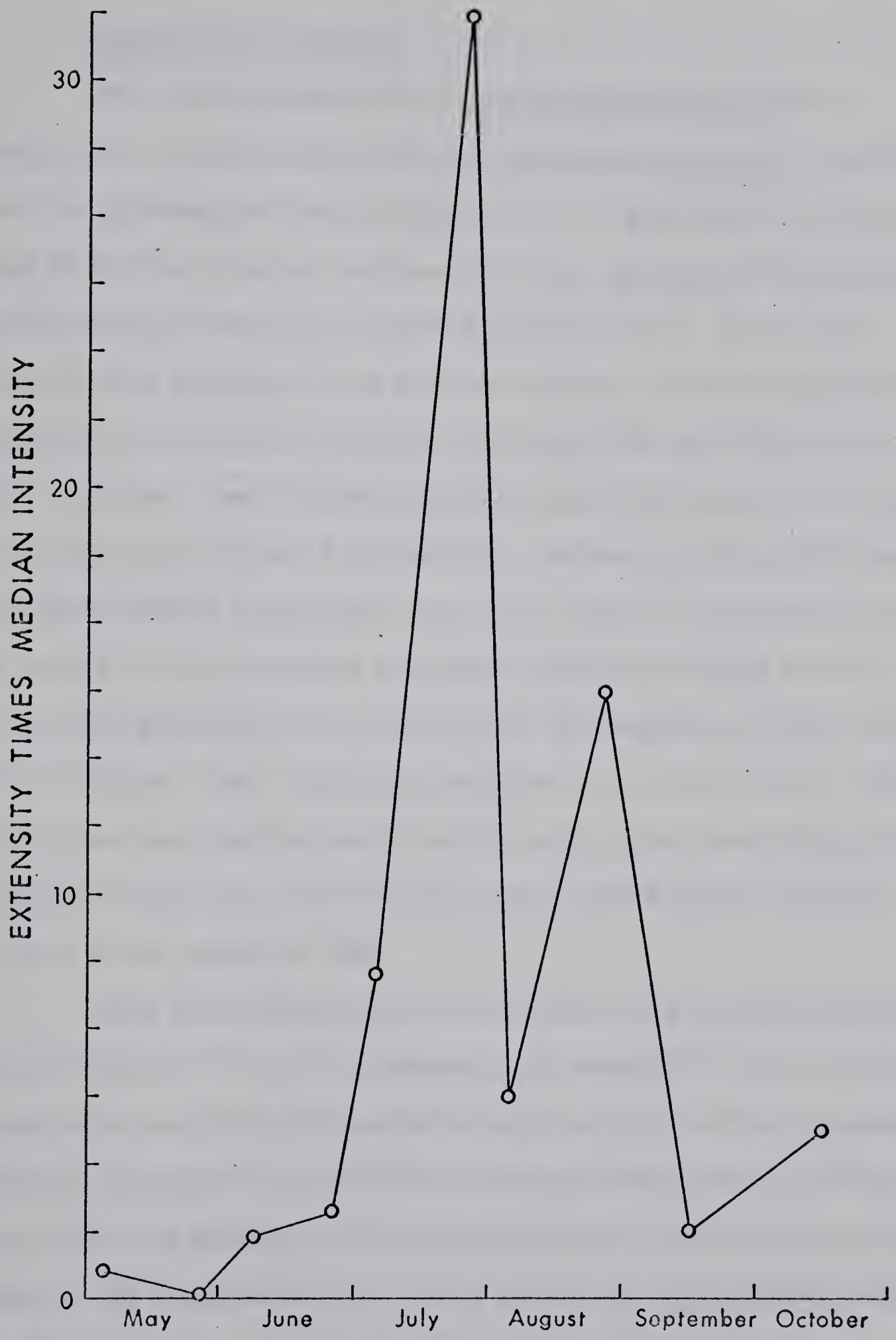

EXTENSITY (PERCENT)
30
20
10
0
April
May
June
July
August
September
October
MONTHS (1966)

Figure 16 Seasonal variation of mature Lateriporus skrjabini in adult lesser scaup (from Graham, 1966)


EXTENSITY TIMES MEDIAN INTENSITY
30
20
10
0
May
June
July
August
September
October

Polymorphus marilis

The seasonal dynamics of Polymorphus marilis are apparently more complex than those of Lateriporus skrjabini, involving both the parental and the young generation of gammarids each year. It would be best to describe the dynamics of P. marilis by following its abundance through the life of a single host generation. It was not possible, in this essentially one year field study, to follow the pattern of abundance throughout the two year maximum life span of the gammarids. However, such a pattern can be constructed from the study of parts of three generations of gammarids: the young gammarids born in 1966 were studied during their first four months of life (until October, 1966), with a few observations during the winter and spring of 1966-1967; the 1965 generation was studied from the beginning of their first winter in October, 1965, through a complete year until October, 1966, with the same few observations in the following winter and spring; and the 1964 generation was studied during their second winter and until their death in the spring of 1966.

Data on acanthellae and cystacanths are presented separately, since the seasonal variation in abundance of acanthellae alone provides information on when the gammarids become infected and the seasonal variation in abundance of cystacanths alone provides a clearer picture of the variation in abundance of material infective to the definitive host. In addition, the acanthellae of the three species of Polymorphus could not be distinguished, hence are combined. Since 88% of the cystacanths were P. marilis and all three acanthocephalans appear to have the same pattern of seasonal abundance, it is assumed that about the same

proportion of acanthellae were P. marilis. In the rest of this section they are treated as if they were all P. marilis; the error should not be significant.

Cystacanths first appeared in the routine samples of the young gammarids (1966 generation) in late July (Fig. 17) although they were first noticed in supplemental examinations on 20 July, some 60 days after their first recruitment. This suggests that at least some gammarids are infected before they are a month old. In experimental infections a laboratory-infected young gammarid only 3.5 mm long was found to harbour an advanced acanthella, and cystacanths were found in gammarids only 7 mm long.

The level of infection increased rapidly, reaching a maximum in mid-August before declining gradually to a lower level in September and October, despite continued infection, as indicated by the appearance of acanthellae (Table XV). Since the young gammarids investigated for parasites in July, August and September were the larger size classes (Table XVI), therefore probably the earliest to be recruited into the population, their incidence of infection would be expected to be greater than in the smaller, younger gammarids that had not been exposed for such a long time to infective eggs. Dilution of the larger size classes with numbers of smaller gammarids might explain the drops in infection in late August and October.

The level of infection in the gammarids during the first winter declined from 2.5% in November and December to 1.0% in March and April (1965 generation; the 1966 generation declined from 5.5% in December to 2.2% in March and April). There was an apparent

selective mortality of those gammarids harbouring a cystacanth. The conditions under the ice became increasingly stagnant through the winter and by March and April no oxygen could be recorded and the level of hydrogen sulphide was high. Menon (1966) reported that these conditions resulted in heavy mortality. It would be reasonable to suggest that the gammarids with the additional stress of a cystacanth would be the likely ones to die.

Immediately after the first appearance of open water in late April, the number of cystacanths increased gradually at first, due to the development of overwintering acanthellae (Fig. 17, Table XV), but then increased sharply 51 - 59 days after breakup. To investigate the possibility that these cystacanths developed from overwintering immature stages not recorded in the routine examinations, about 1000 gammarids were collected from under the ice a month before breakup and placed with lake mud and water in several aquaria in the laboratory at a temperature of 22.5 C. Samples of gammarids were examined at regular intervals. Special attention was paid to looking for acanthors and early acanthellae in these examinations.

The number of acanthors in early samples, the increase in numbers of acanthellae in the middle samples and the subsequent increase in cystacanths in later samples (Table XVII) indicate that the major proportion of the parasite population in gammarids at the end of winter is in the acanthor stage, or that the gammarids were becoming infected in the laboratory.

As a control against the latter, about 200 gammarids from

the same collection had been washed in tapwater and placed in an aquarium with soil from the campus gardens and tapwater, providing an environment free from any possible infective eggs. These gammarids were later autopsied and data on their infections compared with those of the gammarids in the possible egg-containing environment of lake mud and water (Table XVIII). There appeared to be no evidence that the acanthors were acquired in the laboratory. On the contrary, since no acanthors were found in the gammarids maintained on the lake mud from 30 days onwards (Table XVII) it appears that the aquaria contained no infective eggs. The development of the acanthors in the gammarids in late winter apparently provides the large numbers of cystacanths that suddenly occur in late June.

These experiments also provided additional information on the developmental time of the parasite in gammarids; some parasites had not developed beyond the acanthor stage after 22 days and some had not reached the cystacanth stage even after 60 days. Apparently, at laboratory temperature, some of the parasites develop from egg to cystacanth in 34 days and others take more than 60 days.

Gammarids continued to acquire infections at a rapid rate (as indicated by the numbers of acanthellae) through late June or early July (Table XV); the numbers of cystacanths steadily increased to a maximum in mid-August, before rapidly declining during the first two weeks of September (Fig. 17). The extensity of infection reached a low level before ice appeared on the lakes in late October.

The infection level in gammarids at the onset of their

second winter was low (a little over 5%) but, unlike the infections in gammarids during their first winter, this level was maintained, with no further decrease during the course of the winter, until this generation of gammarids died out shortly after breakup.

There were no significant differences in this pattern in the three regular collecting sites (p. 8), each of which had a substantial waterfowl population. However, on two occasions during the summer, gammarids were sampled from the centre of the main body of the lake, some distance from the regular collection sites, and less frequently used by waterfowl; the level of infection with P. marilis in them was significantly lower than in the two regular collection sites (Table XIX).

This pattern of abundance of P. marilis cystacanths in gammarids correlates well with the pattern Graham (1966) found for adult P. marilis in lesser scaup. Graham's data on scaup infections were gathered in 1964 and 1965, those on gammarid infections in 1966; their close fit suggests that the seasonal dynamics of P. marilis are rather constant from year to year.

Lesser scaup apparently did not bring any P. marilis into the region in the spring (the numbers of adults found in ducks shot during breakup are small and no gravid females have been recorded--Graham and Podesta, 1967, personal communication), but acquired their infection entirely from the gammarids in the lakes. The initial gradual rise in the abundance of adults (Fig. 18) probably reflects the ingestion of cystacanths that developed from overwintering acanthellae. Providing there is no selection by the ducks with respect to the size of gammarids they eat, the older (1964) and the younger (1965) generations

would provide equivalent numbers of cystacanths immediately after breakup (Fig. 19; Table XX). However, two weeks after breakup, the older generation completely dies out leaving the younger generation the sole source of cystacanths. Those cystacanths that developed from overwintering acanthors in these gammarids probably contributed the major portion of the adults of their first peak in abundance in the second half of July.

On the basis of the laboratory studies (p. 56), the minimal time for the parasite to complete its full development from cystacanth to cystacanth would be 55 days (21 in the duck and 34 in the gammarid); accordingly, cystacanths derived from eggs voided by ducks that acquired their infection from gammarids immediately after breakup would begin to appear in early July, from whence they would make up an increasing proportion of the cystacanths. The rapid increase in numbers of cystacanths resulting from the development of overwintering acanthors, and the subsequent increase in adults in scaup in July, should be reflected in the numbers of cystacanths in mid-August. Interestingly, the maximum abundance of cystacanths was found in the second half of August!

The marked decline in the abundance of adults in the first half of August probably is, at least in part, a function of a decrease in the number of cystacanths ingested in the second half of July (as a result of the ingestion of large numbers of uninfected young gammarids, which make up the vast majority of the gammarid population at that time), and the loss, due to senescence, of the adults previously present in the ducks. Laboratory experiments indicated that adult males have a life span of 10 - 50 days (26 days) and females 27 - 63 days (44 days). These

periods of time, clearly, may be very different for the adults in natural populations where much larger numbers may influence the life span of individuals or a change in the food habits of the host may result in the elimination of many individuals.

The large numbers of infective eggs that must surely have accompanied the July peak in abundance of adults apparently did not result in the production of many cystacanths in the 1965 generation of gammarids, since as was indicated earlier, very few acanthellae were found in them from mid-July onwards; however, these eggs probably did account for most of the cystacanths in the young gammarids.

The calculations shown in Table XX suggest that by early August the young superseded the parents in importance as a source of infection to the ducks, and possibly the larger proportion of the adults in their second peak of abundance in the second half of August was derived from cystacanths from these young gammarids.

In September and subsequent months, the decline in the number of adults probably results in large numbers of eggs becoming available to the gammarids. These eggs, ingested by the gammarids shortly before the freezeup, survive the winter as acanthors and so provide the major source of infection to ducks the following year.

Thus it appears that most of the adults in the first peak of abundance in the ducks are derived from gammarids infected with eggs from birds of the previous year, and most of the adults of the second peak are derived from gammarids infected with eggs from birds earlier the same year. The majority of the population of P. marilis, then, probably pass through two generations annually.

The first peak of the adults may be regarded as the means whereby the parasite population in the gammarids is switched from the parental generation to the young generation, whilst the second peak provides the overwintering infection.

The seasonal distribution of the cystacanths does not show this bimodal distribution, but rather a single peak in infection terminating at the cold weather of early fall. Since the seasonal distribution of adults indicates that the exposure of the gammarids is probably bimodal in character, the single peak in the gammarids suggests that the life span of the cystacanth and of its host is relatively long, allowing accumulation of infected individuals in the population. Cystacanth-bearing gammarids have lived 7-8 months in the laboratory, suggesting that they do have a relatively long life span. In addition, the data from the experiment on the development of cystacanths in gammarids collected before breakup (p. 89) suggest that not all the acanthors develop at the same rate, which would of course tend to mask a bimodal pattern.

TABLE XV

SEASONAL VARIATION IN POLYMORPHUS ACANTHELLAE IN THE 3 GENERATIONS

Date of collection	1964 generation		1965 generation		1966 generation	
	No. of gammarids	Extensity of infection	No. of gammarids	Extensity of infection	No. of gammarids	Extensity of infection
Oct/65	48		436	0.9		
Nov	65		433	0.7		
Dec	55	1.8	605	0.3		
Jan/66	77	1.3	420	0.7		
Feb	56		498	1.0		
Mar	106		608	0.3		
Apr 30	29		274			
May 7	3		209	1.9		
May 17			313	1.3		
May 21			383	2.1		
May 31			338	9.2		
Jun 7			198	14.1		
Jun 14			100	13.0		
Jun 20			100	23.0		
Jun 29			238	14.7	75	
Jul 6			102	13.7	86	
July 11			284	2.1		
Jul 20			93	1.1	62	
Jul 29			196	2.0	41	
Aug 4			177	0.6	250	1.6
Aug 10			219	0.5	30	
Aug 23			149		50	
Aug 31			163		41	2.4
Sept 14			116		88	
Sept 23			41	2.4	147	4.8
Oct			46	4.3	548	2.6
Dec			14	7.1	186	1.6
Mar/67			8		180	1.1

TABLE XVI

EXTENSITY OF POLYMORPHUS MARILIS IN THE LARGER SIZE CLASSES OF YOUNG GAMMARIDS (1966 GENERATION)

Date of collection	Size classes (mm.)	No. of gammarids	% infected
June 29	4, 5, 6	75	-
July 6	5, 6, 7, 8	86	-
July 20	7, 8, 9	62	-
July 29	9, 10	41	2.5
August 4	9, 10, 11	250	5.2
August 10	10, 11	30	20.0
August 23	10, 11, 12	50	10.0
August 31	10, 11, 12	41	2.4
September 14	10, 11, 12, 13	88	6.8
September 23	10, 11, 12, 13	147	8.8
October	10, 11, 12, 13	393	5.6
	6, 7, 8, 9	155	3.2

TABLE XVII

DEVELOPMENTAL STAGES OF POLYMORPHUS MARILIS FROM A COLLECTION OF GAMMARIDS FROM UNDER THE ICE AND MAINTAINED IN THE LABORATORY

Days after collection	Stage of development	Male No.	Male Ext.	Female No.	Female Ext.	Under 10 mm. long No.	Under 10 mm. long Ext.	Total No.	Total Ext.
less than	cystacanth		5.1		1.5		-		2.7
24	acanthella	78	2.6	67	-	43	-	188	1.1
hours	acanthor		9.0		4.5		2.3		5.9
	cystacanth		11.5		7.6		-		8.5
14*	acanthella	78	7.7	79	6.3	19	-	176	6.3
	acanthor		6.4		6.3		-		5.7
	cystacanth		11.3		1.2		-		5.3
22*	acanthella	62	17.7	82	9.7	6	-	150	12.6
	acanthor		1.6		4.8		-		3.3
	cystacanth		20.8		7.5		-		14.3
30	acanthella	72	12.5	66	9.0	1	-	139	10.7
	acanthor		-		-		-		-
44	cystacanth	78	30.8	40	15.0	-	-	118	25.4
	acanthella		9.0		2.5		-		6.8
60	cystacanth	40	35.0	31	19.4	-	-	71	28.3
	acanthella		5.0		-		-		2.8

*Combined data from Table XVIII

This experiment is more fully described in the text pages.

TABLE XVIII

DEVELOPMENTAL STAGES OF POLYMORPHUS MARILIS IN GAMMARIDS MAINTAINED IN THE LABORATORY AQUARIA WITH LAKE MUD AND LAKE WATER OR WITH GARDEN SOIL AND TAPWATER

Days after collection	Stage of development	Gammarids with mud and water from Cooking Lake		Gammarids with garden soil and tapwater	
		No.	Ext.	No.	Ext.
	cystacanth		10.0		6.6
14	acanthella	100	8.0	76	4.9
	acanthor		4.0		7.9
	cystacanth		6.1		3.9
22	acanthella	99	12.1	51	13.7
	acanthor		3.0		3.9

TABLE XIX

EXTENSITY OF POLYMORPHUS MARILIS IN GAMMARIDS FROM THE CENTRE OF THE LAKE VERSUS REGULAR COLLECTION SITES

July 6, 1966

	Male		Female		Total	
	No.	Ext.	No.	Ext.	No.	Ext.
Centre of lake	37	19.0	75	10.7	110	13.6
Collection site	63	52.4	39	23.1	102	41.0

$x^2 = 16.9$; d.f. = 1; p.01 = 6.64

July 29, 1966

	Male		Female		Total	
	No.	Ext.	No.	Ext.	No.	Ext.
Centre of lake	38	36.8	62	11.3	100	21.0
Collection site	70	35.7	128	31.3	198	32.8

$x^2 = 8.5$; d.f. = 1; p.01 = 6.64

TABLE XX

SEASONAL VARIATION IN THE PROPORTION OF POLYMORPHUS MARILIS CYSTACANTHS IN THE THREE GAMMARID GENERATIONS

	1964			1965			1966	
	Percent of gammarid population	Extensity	Percent of cystacanth population	Percent of gammarid population	Extensity	Percent of cystacanth population	Percent of gammarid population	Extensity	Percent of cystacanth population
Oct	9.9	4.1	9.2	90.1	4.4	90.8			
Nov	13.1	7.7	24.8	86.9	3.5	75.2			
Dec	8.3	3.6	11.5	91.7	2.5	88.5			
Jan	15.5	5.2	35.9	84.5	1.7	64.1			
Feb	10.1	5.4	23.2	89.9	2.0	76.8			
Mar	14.8	6.6	48.6	85.2	1.3	51.4			
Apr	9.6	6.9	57.0	90.4	1.1	43.0			
May 1	1.4	0	0	98.6	3.3	100.0			
May 2	0			100.0	4.5	100.0			
May 3					7.3				
May 4					4.1				
Jun 1					8.6				
Jun 2					13.0				
Jun 3					13.0				
Jun 4					29.0			0	
Jul 1		5.0	41.0	100.0		95.0	0		0
Jul 2		5.0*	33.1	100.0			0		0
Jul 3		5.0	50.5	100.0		95.0	0		0
Jul 4		4.0	33.2	35.6		96.0	2.5		64.4
Aug 1		4.0*	50.3	28.7		96.0*	5.2		71.3
Aug 2		5.0	49.5	11.5		95.0	20.0		88.5
Aug 3		5.0*	62.0	24.6		95.0*	10.0		75.4
Aug 4		5.0*	46.0	50.2		95.0*	2.4		49.8
Sept 1		7.0*	21.6	19.2		93.0*	6.8		80.8
Sept 2		8.0*	29.3	22.4		92.0*	8.8		77.6
Oct		10.5	28.3	41.9		89.5	4.6		58.1
Dec		7.0	7.1	9.7		93.0	5.5		90.3
Mar/67		4.3	12.5	25.5		95.7	2.2		74.5

*estimated percentages (data from Menon, 1966)

Figure 17 Seasonal variation in extensity of Polymorphus marilis cystacanths

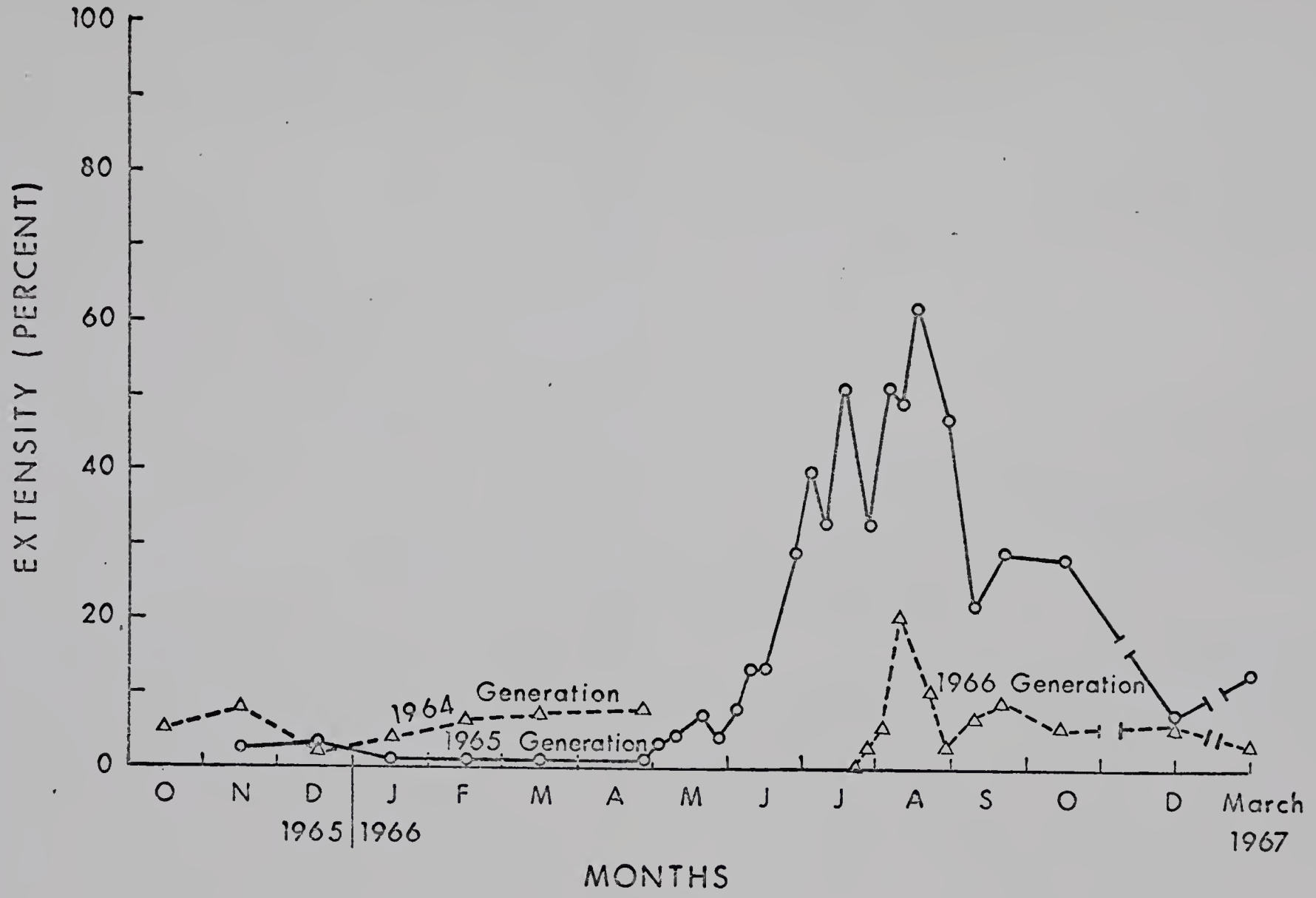

EXTENSITY (PERCENT)
100
80
60
40
20
0
1964 Generation
1965 Generation
1966 Generation
O N D J F M A M J J A S O D March
1965 1966 1967
MONTHS

Figure 18 Seasonal variation in Polymorphus marilis in adult lesser scaup (replotted from Graham, 1966)

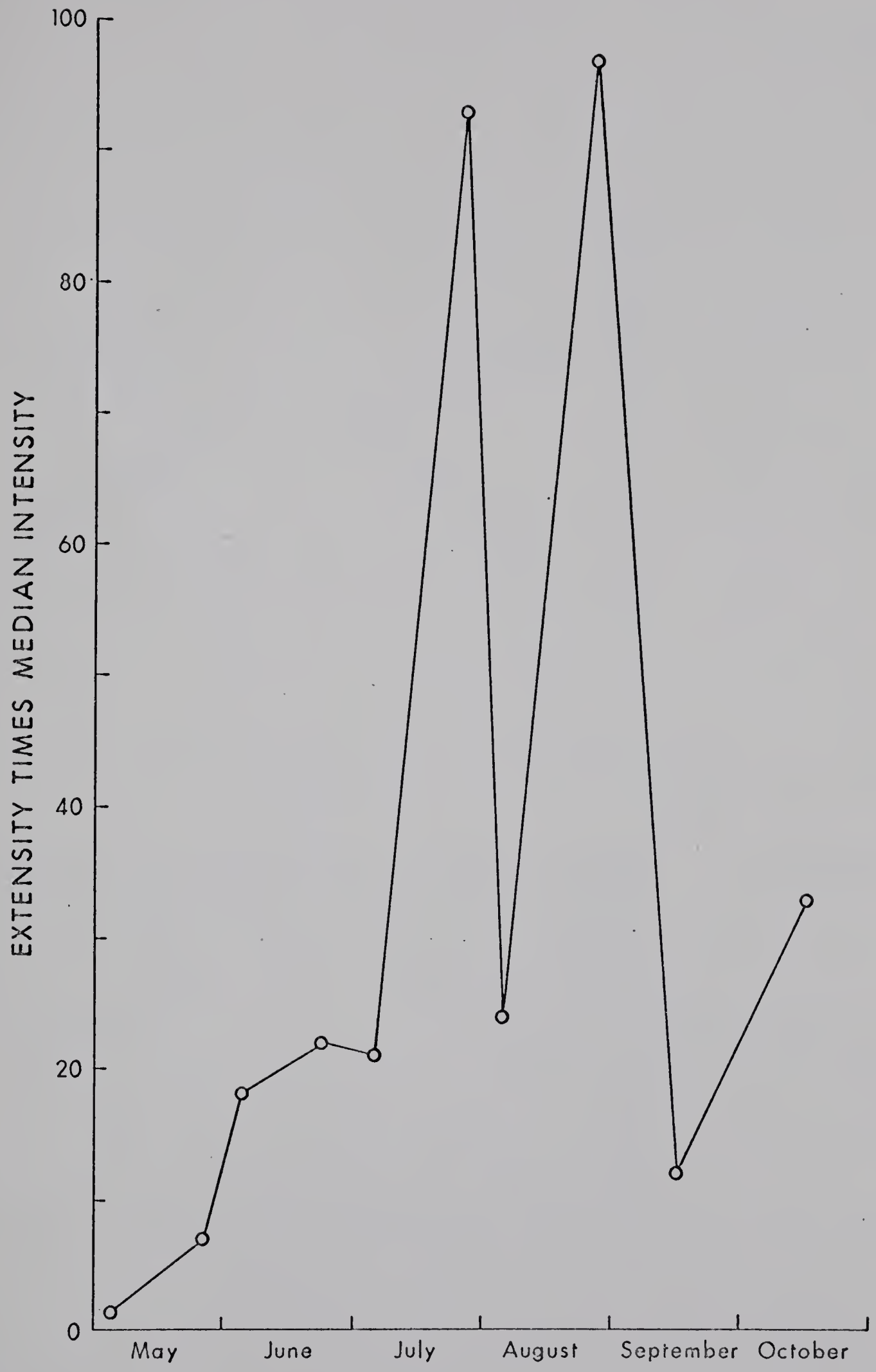
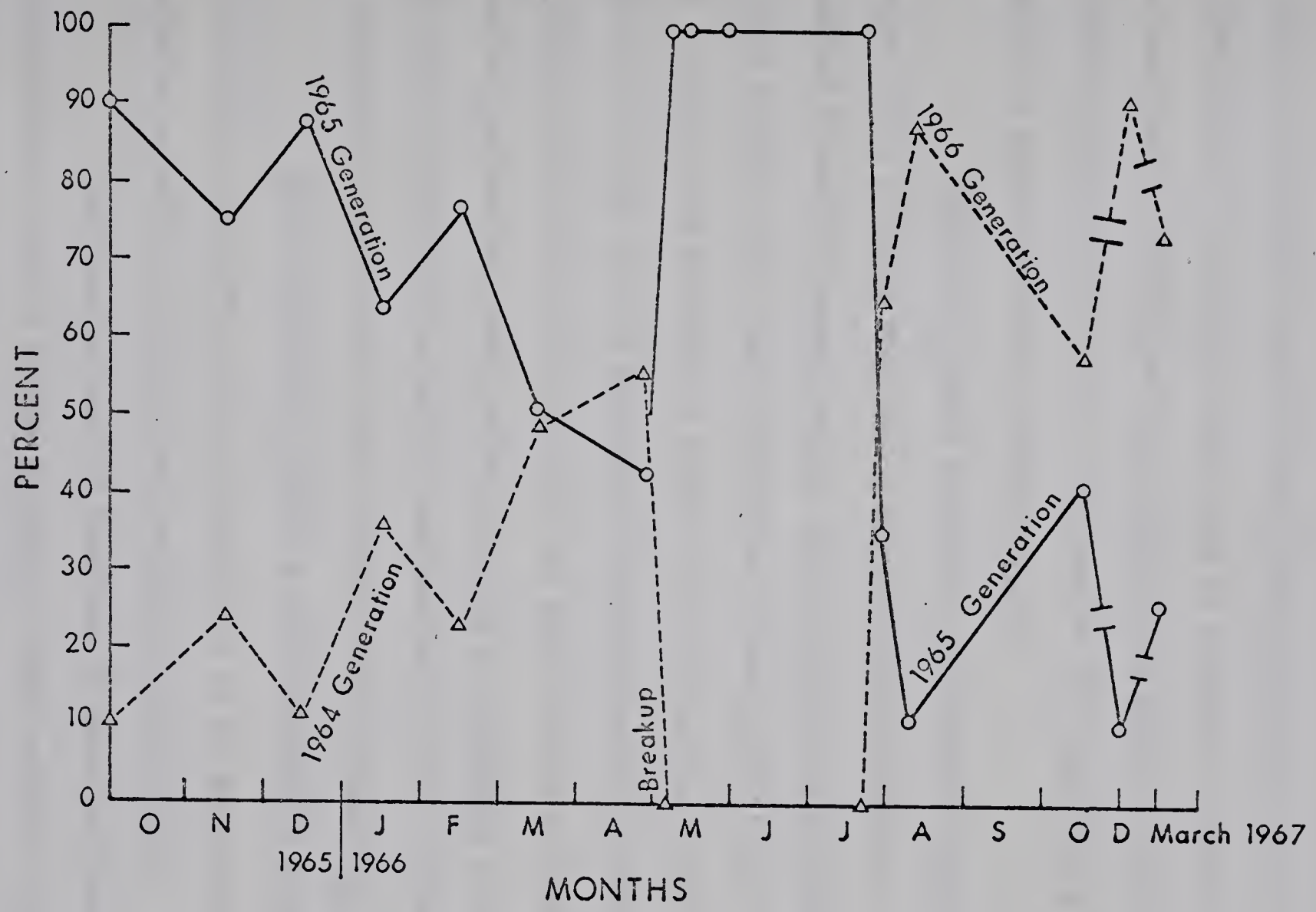

EXTENSITY TIMES MEDIAN INTENSITY
100
80
60
40
20
0
May
June
July
August
September
October

Figure 19 Seasonal variation in the proportion of Polymorphus marilis cystacanths maintained in the three gammarid generations


100
90
80
70
60
50
40
30
20
10
0
PERCENT
1965 Generation
1964 Generation
1966 Generation
1965 Generation
Breakup
O N D J F M A M J J A S O D March 1967
1965 1966
MONTHS

Mortality of Infected Gammarids

The life spans of the cysticercoids, cystacanths and juvenile nematodes are probably wholly dependent upon how long the infected gammarids live; there was no evidence of death or absorption of such larvae within the body cavity of the hosts. The longer the infected gammarids survive, the greater the opportunity the larvae have for ingestion by the definitive host.

There was some evidence, mostly discussed in previous pages, that infected individuals have shorter life spans, or were more subject to environmental stress, than uninfected ones; namely, the rapid decline in the rate of infection of gammarids with cystacanths of P. marilis with the drop in temperature at the end of the summer, the decrease in the rate of infection of gammarids with cystacanths of P. marilis during their first winter, the rapid declines in the infection rate of gammarids with cysticercoids of L. skrjabini from peaks of abundance during the summer, and laboratory observations of the short life spans of gammarids infected with cysticercoids of L. skrjabini.

Some additional evidence may be obtained from consideration of the relationship of the sex and size of the gammarids to the relative survival of infected and uninfected gammarids.

The general level of infection of male and female gammarids with the three species of Polymorphus, three species of Lateriporus and the species of Hymenolepis (treated together) is shown in Table XXI.

The fact that no significant differences between these infection rates were found in most of the species suggests that there was no

difference in the rate of exposure between the sexes. However, Lateriporus skrjabini, and Polymorphus paradoxus, both large parasites, had significantly higher infection rates in male gammarids, suggesting that infected females have a shorter life span than infected males.

Polymorphus paradoxus cystacanths were not found frequently enough to warrant further analysis of the data on them. Lateriporus skrjabini, however, were abundant. Their extensity in male gammarids is higher than that in the females throughout the entire period of infectivity (Fig. 20), particularly during the peak reproductive period of the females in June. Only rarely were infected ovigerous females observed, and in four out of the five so found, the number of eggs in the brood pouch were noticeably less than normal. This is in agreement with the casual observations made by Menon (1966). Perhaps the large size of the cysticercoids interferes with ovarian function in some way that results both in a decrease in the number of eggs in the brood pouch and in an increase in the chance of death by the host. By inducing mortality among ovigerous females Lateriporus skrjabini might play some part in limiting the biotic potential of the gammarid population.

Although there was no significant difference in the infection rates of the male and female gammarids of the total population throughout the year period with Polymorphus marilis (Table XXII), a great deal of variation in the relative infection rates of males and females was observed in the different generations at different times of the year (Table XXIII). Selective mortality of infected female gammarids was greatest in the 1965 generation during May and June and in the same

generation during November to April. On both occasions the females may have been under considerable additional stress; the first due to their state of reproduction (ovigerous - Fig. 14) and the second due to the effects of the winter (females do not survive their first winter as well as males - Menon, 1966). An interesting reversal in "sex selection" of infected gammarids was noticed in the overwintering 1964 generation (gammarids in their second winter) when the females were found to be nearly twice as heavily infected as the males!

The relationship between the infection rate and the size of the gammarids was investigated in three different stages of the life history.

The larger size classes of young were three times more heavily infected with Polymorphus marilis than the smaller size classes in October (Table XVI). This is probably a function of the greater exposure of the larger, presumably older gammarids.

The larger and smaller size classes of the 1965 generation during the period of high infection rates in the summer show about the same level of infection (Fig. 21). This is in contradistinction with the observation of Hynes (1955) in which gammarids infected with Polymorphus minutus were generally smaller than the uninfected ones of the same generation. Hynes suggested that his data indicated the acanthocephalan delayed the growth of their hosts. Clearly, no such delay was evident in the present study.

During the winter, gammarids of the larger size classes (1964 generation) were more heavily infected with Polymorphus marilis than those of the smaller size classes (1965 generation) and, moreover,

the infected individuals of larger gammarids survived the winter better than those of the smaller ones (Table XXIV). Hynes (1955) showed that infected larger gammarids survived the winter better than infected smaller individuals of the same generation. In this study, however, the larger and smaller size classes of the 1965 generation had very similar levels of infection during the winter.

During the winter months, then, there appears to have been no differential mortality between larger and smaller infected gammarids of the younger (1965) generation, but there was a differential mortality between the infected gammarids of the two overwintering generations.

TABLE XXI

COMPARISON OF INFECTION RATES IN MALE AND FEMALE GAMMARIDS

	Extensity		X^2 (b)
	Male gammarids	Female gammarids	
Polymorphus contortus (a)	1.7	1.5	1.19
Polymorphus marilis	14.0	13.0	1.34
Polymorphus paradoxus (a)	2.2	1.0	15.5
Lateriporus clerci	0.2	0.1	1.81
Lateriporus mathevossianae	0.8	0.5	2.39
Lateriporus skrjabini (a)	19.0	7.6	186.2
Hymenolepis spp.	0.8	0.6	0.83

(a) based on 1683 males, 1760 females; others based on 3289 males, 3463 females. These are the numbers of gammarids examined during the period when the parasite was present.

(b) X^2 (1 d.f.) p(0.05) = 3.84, p (0.01) = 6.64

TABLE XXII

EXTENSITY OF INFECTION WITH POLYMORPHUS MARILIS AND THE SEX OF THE GAMMARIDS

Date of collection	1964 Generation male No.	1964 Generation male Ext.	1964 Generation female No.	1964 Generation female Ext.	1965 Generation male No.	1965 Generation male Ext.	1965 Generation female No.	1965 Generation female Ext.	1966 Generation male No.	1966 Generation male Ext.	1966 Generation female No.	1966 Generation female Ext.
Oct/65	24	4.2	24	4.2	103	5.8	191	4.7				
Nov	43	7.0	22	9.1	163	5.5	137	2.2				
Dec	34	2.9	21	4.8	132	2.3	182	2.7				
Jan/66	55	5.5	22	4.5	233	1.3	136	2.9				
Feb	39	2.6	17	11.8	210	2.4	196	2.0				
Mar	68	2.9	38	14.3	238	2.9	206	1.0				
Apr 30	28	7.1	1	-	144	1.4	124	0.8				
May 7	2	-	1	-	166	8.6	31	-				
May 17					88	8.0	148	2.7				
May 21					157	8.3	173	2.9				
May 31					136	5.9	121	4.1				
Jun 7					99	12.0	91	5.5				
Jun 14					64	14.0	36	11.1				
Jun 20					45	13.3	55	12.7				
Jun 29					121	38.0	117	19.7				
Jul 6					63	52.4	39	23.1				
Jul 11					120	40.0	164	28.0				
Jul 20					22	63.6	71	48.5				
Jul 29					65	36.9	131	30.5	5	20.0		
Aug 4					73	50.7	104	50.0	32	9.4		
Aug 10					90	51.1	129	47.3	30	20.0		
Aug 23					51	70.6	98	57.3	34	3.0	16	25.0
Aug 31					69	40.6	94	51.1	39	2.6	2	-
Sept 14					60	28.3	56	14.3	69	7.2	19	5.3
Sept 23					27	29.6	14	28.6	90	10.0	57	7.0
Oct					27	29.6	19	26.3	151	7.9	242	4.1
Dec					10	10.0	4	25.0	89	10.1	74	6.8
Mar/67					7	-	1	-	80	3.4	70	1.5

TABLE XXIII

COMPARISON IN INFECTION RATES IN MALE AND FEMALE GAMMARIDS WITH POLYMORPHUS MARILIS IN DIFFERENT GENERATIONS AT DIFFERENT TIMES OF THE YEAR

Generation	Sample period	Males No. sampled	Ext.	Females No. sampled	Ext.	X^2	Probability
1966	Jul-Dec	539	8.7	410	5.8	2.84	0.05 p 0.10
1965	Nov-Apr	1120	2.0	981	1.2	1.88	0.10 p 0.20
	May-Jun	876	12.2	772	6.8	1.25	0.20 p 0.30
	Jul-Aug	553	48.1	825	41.9	13.39	p 0.01
1964	Nov-Apr	267	4.4	111	8.1	5.07	0.02 p 0.05
X^2 for homogeneity of sub-samples (expected based on the overall extensity of P. marilis - 12.7%)				(9 d.f.)		1360.3	p (0.01) = 21.67

TABLE XXIV

RELATIVE OVERWINTERING SURVIVAL OF POLYMORPHUS MARILIS INFECTED GAMMARIDS OF THE TWO GENERATIONS

Period of sample	1964 generation No. of gammarids	1964 generation Percent infected	1965 generation No. of gammarids	1965 generation Percent infected
Nov. and Dec.	120	5.8	1038	2.9
Mar. and Apr.	135	6.7	882	1.2

X^2 (1964 generation) = 0.05; d.f. = 1; p 0.01 = 6.64

X^2 (1965 generation) = 6.10; d.f. = 1; p 0.01 = 6.64

Figure 20 Rate of infection with Lateriporus skrjabini and the sex of the gammarids (1965 generation)

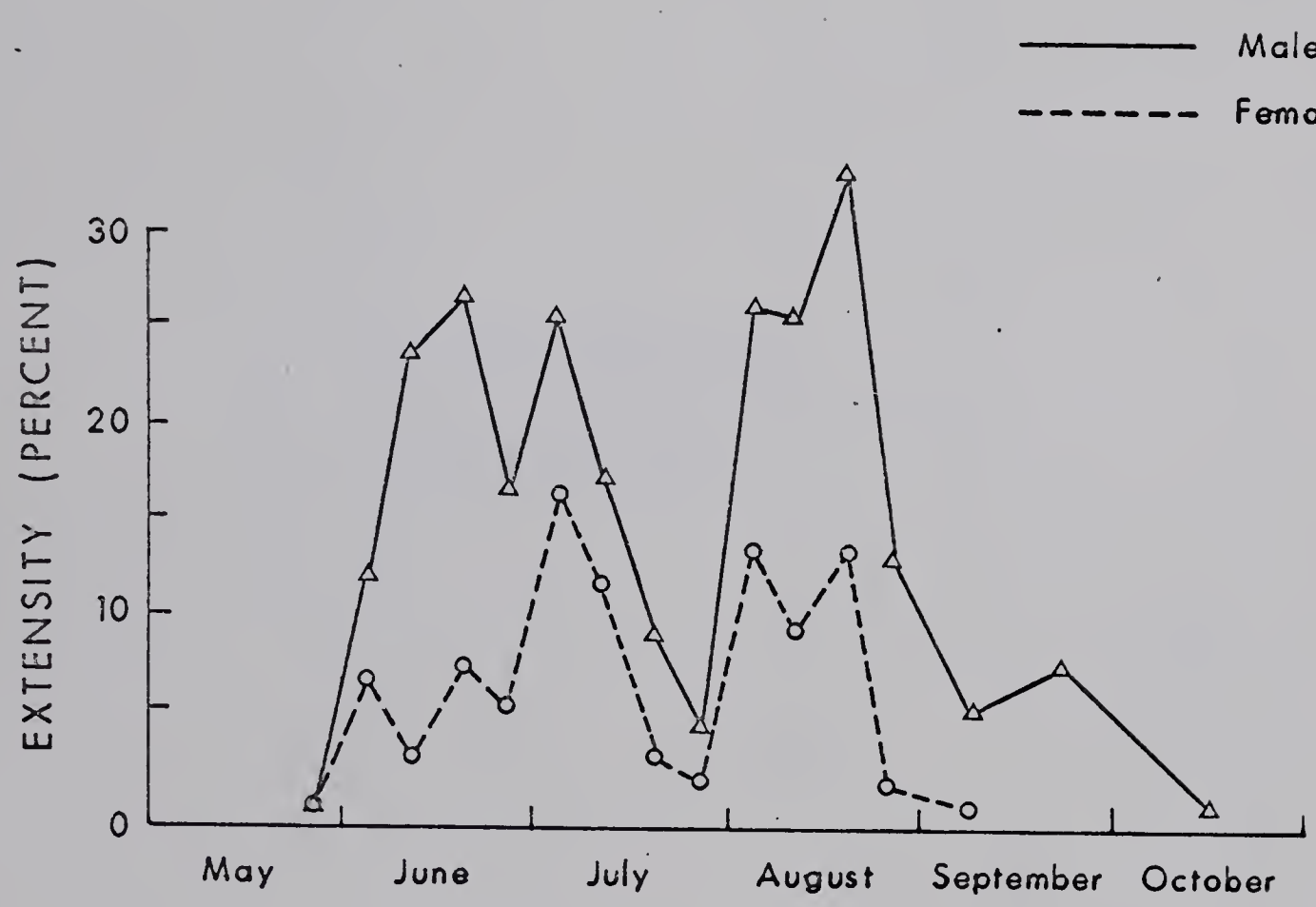
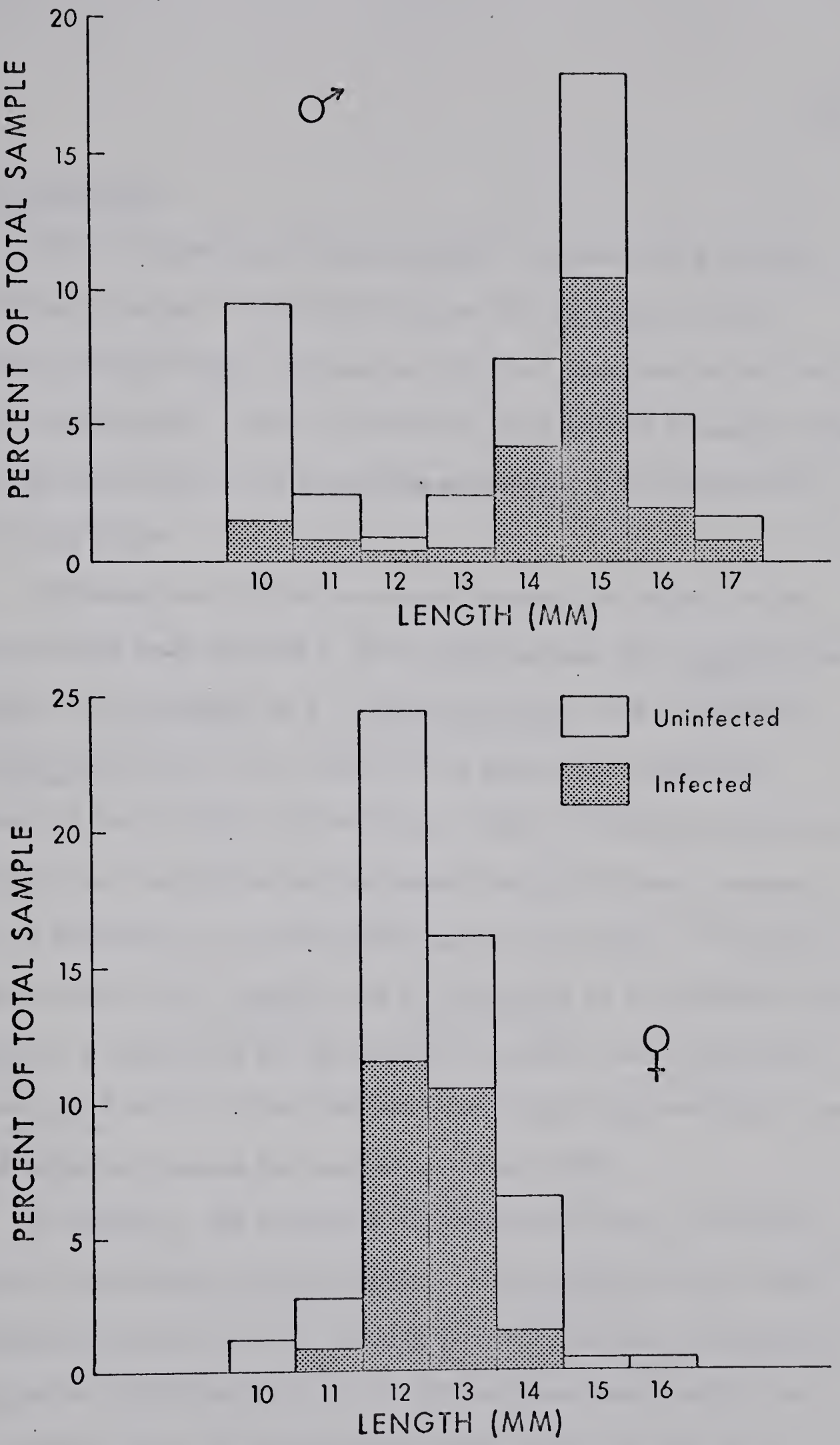

Male gammarids
Female gammarids
EXTENSITY (PERCENT)
30
20
10
0
May
June
July
August
September
October

Figure 21 Size distribution of infected gammarids and those uninfected with cystacanths of Polymorphus marilis (sample taken on 10th August 1966, comprising of 102 males and 147 females)


♂
PERCENT OF TOTAL SAMPLE
0
5
10
15
20
10
11
12
13
14
15
16
17
LENGTH (MM)
Uninfected
Infected
♀
PERCENT OF TOTAL SAMPLE
0
5
10
15
20
25
10
11
12
13
14
15
16
LENGTH (MM)

Concurrent Infections

All combinations of the helminths encountered probably occur in the gammarids. Table XXV shows the frequency of the combinations actually found, compared with that expected on the basis of a random association. Clearly, there is no evidence to suggest that prior infection with any of the helminths precludes a superimposed infection by any other.

Although none of the observed frequencies appear to be significantly lower than expected, four combinations (P. marilis plus P. paradoxus, L. skrjabini or L. mathevossianae; and acanthellae plus L. skrjabini) appear to be higher than expected, suggesting enhancement of one parasite by the other. These differences however, are apparently due largely to the parasites having different seasonal variations in abundance, but with peaks at the same time. When the expected infections of P. marilis and L. skrjabini or acanthellae and L. skrjabini are calculated for the summer months, the only period when L. skrjabini occurs, then the observed values approximate more closely the expected values (in brackets, Table XXV).

In addition, the observed combined infection of the two most common helminths, P. marilis and L. skrjabini, for each week over the summer period is very similar to the theoretical frequency based on random infections (Fig. 22). Chi-square tests indicate no significant differences between the observed and expected values, either for the entire period or for the four weeks of greatest disparity between the observed and expected values. Laboratory infections also indicate that infections, at least with some of the parasites, occur as

frequently in gammarids previously infected (mostly with P. marilis or L. skrjabini) as they do in previously uninfected individuals (Table XXVI). Clearly, there appears to be no interaction between helminths insofar as extensity is concerned.

Analysis of the interaction between P. marilis and L. skrjabini during July and August indicate that the intensity of infections of the two helminths is also unaffected by concurrent infection (Table XXVII).

Concurrent infections of acanthellae with mature lateriporid cysticercoids and of immature lateriporid cysticercoids with cystacanths might indicate arrested or hindered development of the acanthellae or immature cysticercoids. If so, the observed frequency of such concurrent infections should be greater than expected. When the summer data are used, no such difference is seen (Table XXV, using the bracketed expected frequency). Also laboratory data from experimental infection of gammarids do not indicate that the rate of development of any of the helminths is impeded by the presence of another helminth species.

Michajlow (1958) studied the interspecific relations between the procercoids of Triaenophorus lucii and the cysticercoids of Drepanidotaenia lanceolata in the copepods, Cyclops strenuus and C. vicinus. He found that concurrent infections, both simultaneous and successive, were always possible, irrespective of their order or interval between the first and second infection; also the extensity of concurrent infections is approximately what would be predicted by the extensity of each cestode separately. Clearly, any one invertebrate host can be invaded

with several species of larvae which appear not to interfere with one another.

TABLE XXV

CONCURRENT INFECTIONS FOUND IN 7135 GAMMARIDS COLLECTED FROM OCTOBER 1965 TO SEPTEMBER 1966

		observed frequency	expected frequency
P. marilis	- L. skrjabini	71	33.6 (90.8)
P. (acanthellae)	- L. skrjabini	17	7.4 (16.4)
P. marilis	- L. mathevossianae	15	6.3
P. marilis	- P. paradoxus	14	7.2
P. marilis	- P. contortus	6	7.2
L. (immature)	- P. marilis	6	5.2
P. marilis	- Hymenolepis B	5	4.5
L. skrjabini	- L. mathevossianae	3	1.8
L. (immature)	- Hymenolepis B	3	0.2
P. marilis	- Hymenolepis A	3	1.8
P. (acanthellae)	- L. (immature)	3	1.4
L. skrjabini	- Hymenolepis B	2	1.3
L. mathevossianae	- Hymenolepis B	1	0.2
L. skrjabini	- P. contortus	1	2.1
L. skrjabini	- P. paradoxus	1	2.1
P. contortus	- P. paradoxus	1	0.4
P. marilis	- L. clerci	1	1.8
P. marilis	- S. crassicauda	1	0.9
P. marilis - L. skrjabini	- Hymenolepis B	1	1.7
P. marilis	- P. paradoxus	1	0.4
P. marilis - L. skrjabini	- Hymenolepis A	1	0.7
P. (acanthellae)	- L. clerci	1	0.4
P. (acanthellae)	- Hymenolepis A.	1	0.4
P. (acanthellae) - L. mathevossianae	- L. skrjabini	1	0.5

TABLE XXVI

EXPERIMENTAL INFECTIONS IN GAMMARIDS WITH OR WITHOUT PREVIOUS INFECTIONS

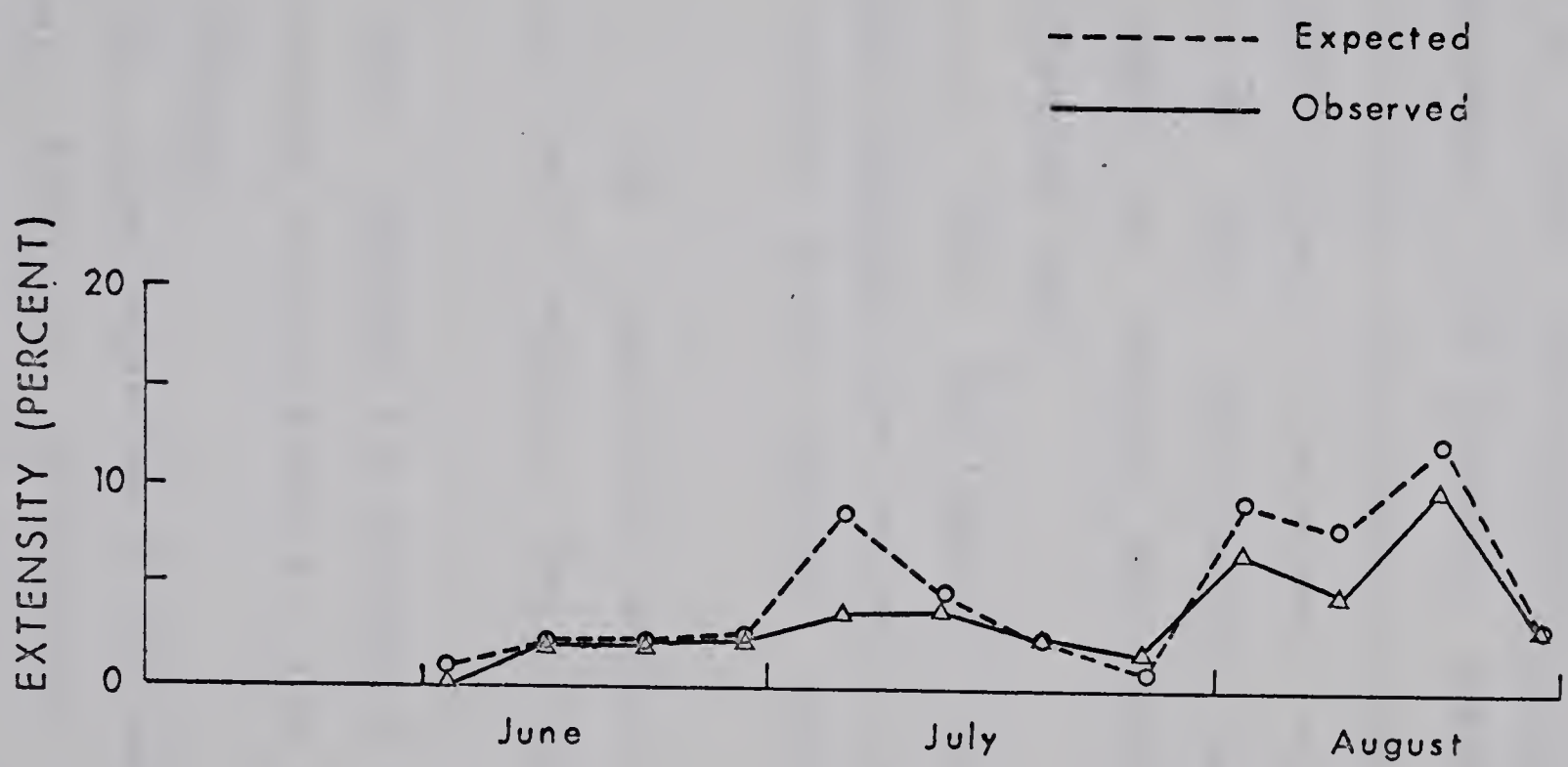
	Gammarids previously uninfected		Gammarids previously infected	
	No.	percent infected	No.	percent infected
L. mathevossianae	74	60.8	8	50.0
L. skrjabini	39	92.3	9	77.8
Hymenolepis B	58	37.9	20	30.0
P. marilis	37	94.6	4	100.0

TABLE XXVII

INTENSITY OF INFECTIONS OF POLYMORPHUS MARILIS AND LATERIPORUS SKRJABINI IN SINGLE AND CONCURRENT INFECTIONS DURING JULY AND AUGUST

	Single			Concurrent		
	No. of infected gammarus	Total No. of parasites	mean intensity	No. of infected gammarus	Total No. of parasites	mean intensity
L. skrjabini	126	413	3.1	67	234	2.9
P. marilis	545	674	1.2	67	81	1.2

Figure 22 Seasonal frequency of concurrent infections of Lateriporus skrjabini and Polymorphus marilis


Expected
Observed
EXTENSITY (PERCENT)
20
10
0
June
July
August

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